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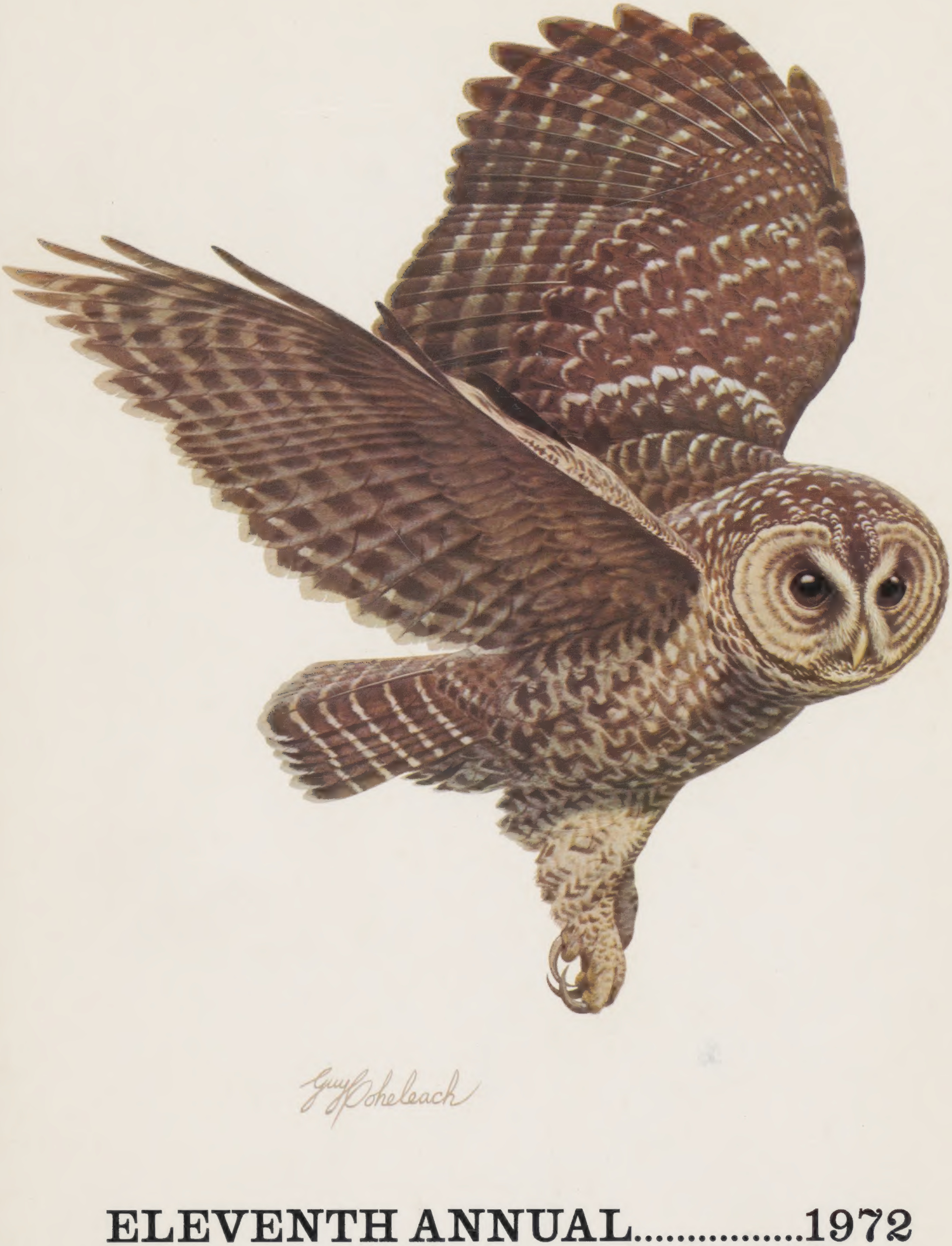
# THE LIVING BIRD


Guy Coheleach

**ELEVENTH ANNUAL................1972**

*Cornell Laboratory of Ornithology*

# THE LIVING BIRD

## ELEVENTH ANNUAL

of the

## Cornell Laboratory of Ornithology

1972

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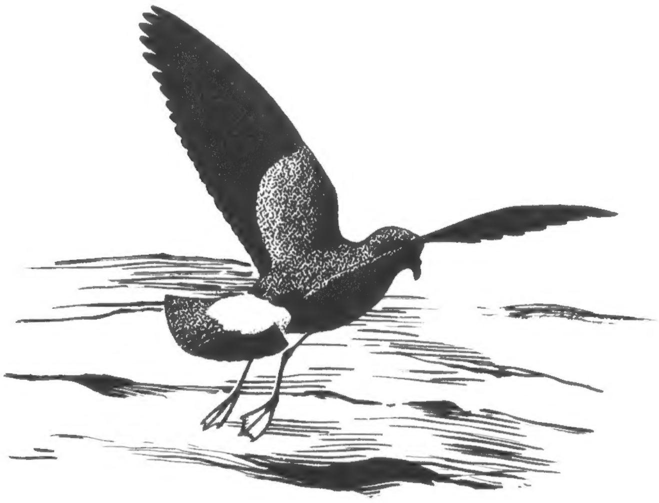
*and*

DOUGLAS A. LANCASTER



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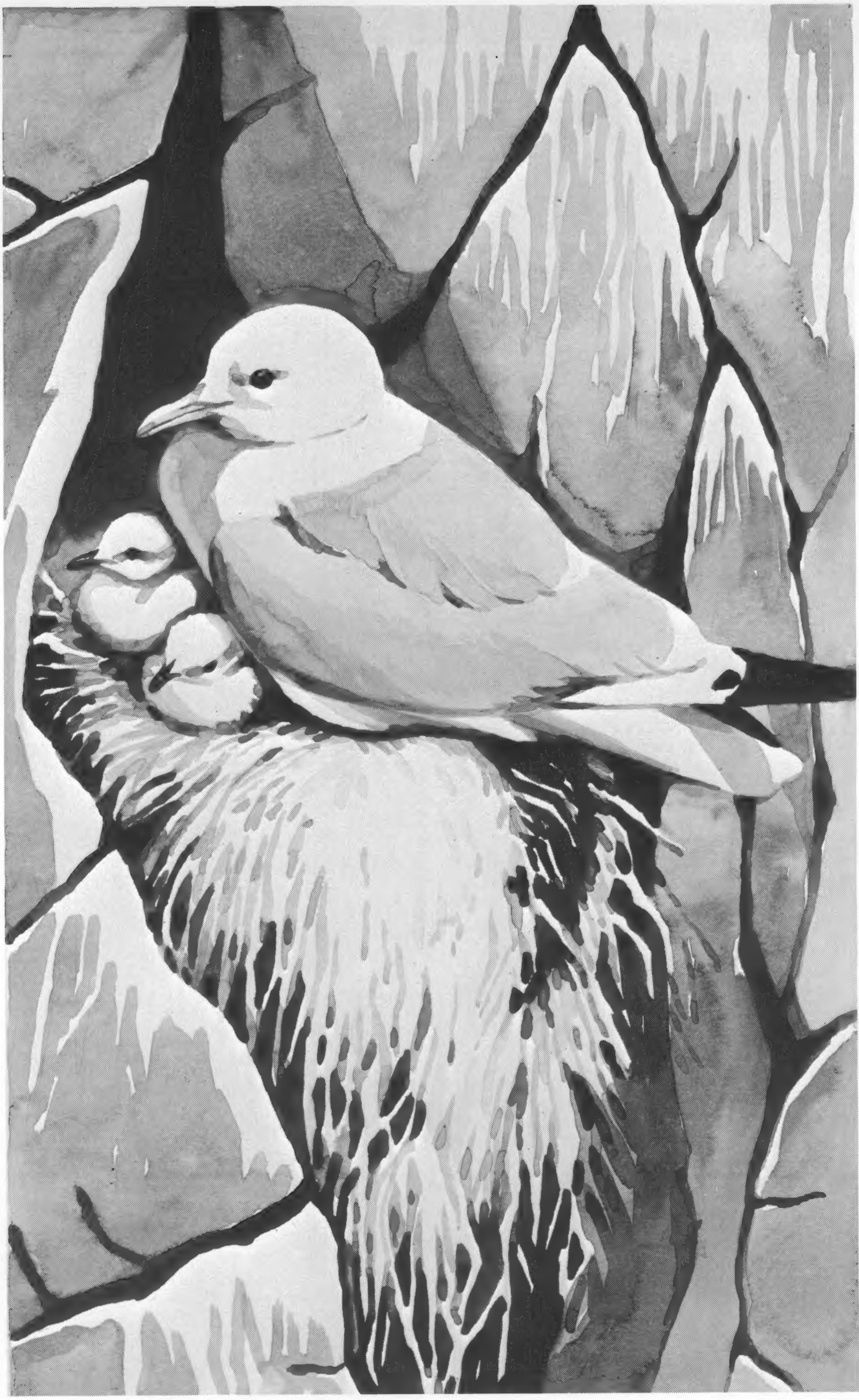

Kittiwake, *Rissa tridactyla*. Painting by N. W. Cusa.

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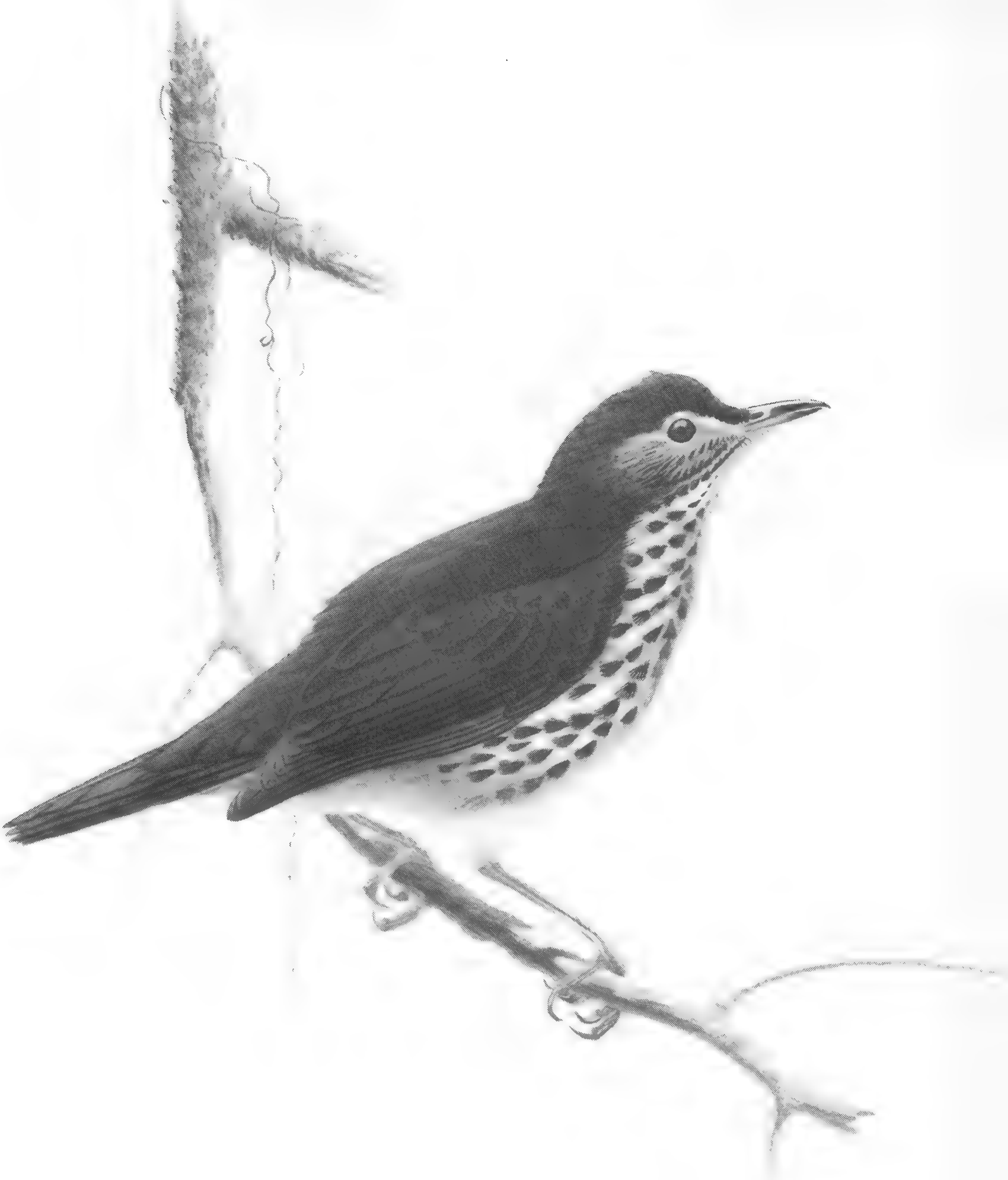

Wood Thrush, *Hylocichla mustelina*. Painting by John O'Neill.

# THE BREEDING BIOLOGY OF THE PINON JAY

Russell P. Balda and Gary C. Bateman

Piñon Jays (*Gymnorhinus cyanocephalus*) are noisy, restless, and gregarious. Even casual observers are impressed by the flocks, sometimes numbering from 50 to 500, of these deep blue birds, all calling loudly and streaking off in long lines. In fall and winter, flights are generally one to three miles in distance. The ranchers in New Mexico wondered how they bred because the birds never seemed to stop moving long enough to nest (Jensen, 1926).

The breeding range of the Piñon Jay extends from Oregon and Montana south to northern Baja California, central Arizona, southern New Mexico, and southwestern Texas. The eastern edge of its breeding range includes western Oklahoma, Colorado, and the western tip of South Dakota (Bent, 1946; AOU Check-list, 1957). Once called Maximilian's Jay after its discoverer, it now bears an equally distinguishing name. Although a number of birds are named after a particular genus of plants, we know of no other North American bird named after a particular subgeneric group of trees, the four piñon pines of the United States belonging to the subsection *Cembroides* of the subgenus *Strobus* (Little and Critchfield, 1969). The name, Piñon Jay, indicates a strong association with, or reliance upon, piñon pine; yet the species' breeding range extends much farther north than the piñon pines and not nearly as far south (Little, 1971). The Piñon Jay, at the northern limits of its range, is closely associated with ponderosa pine (*Pinus ponderosa*). Braly (1931) described the Piñon Jay nesting in ponderosa pines in Oregon.

This report, covering four years from 1968 to 1971, deals specifically with some aspects of the breeding activities of a flock that varied in size from about 250 birds to 125. We reported on the annual flocking cycle of this group elsewhere (Balda and Bateman, 1971).

## *Study Area*

We worked in the vicinity of Flagstaff, Arizona, at elevations from approximately 6,500 to 7,000 feet. In February 1968, we began observations on a flock — the Doney Park Flock — of about 250 individuals 10 miles northeast of town; in February 1971, we began observations on a somewhat smaller flock — the Town Flock — living in Flagstaff and adjacent natural areas; and we followed the reproductive activities of both flocks through the 1971 nesting season. Data from the Doney Park Flock, studied most intensively, form the basis of most of our conclusions.

The home range of the Doney Park Flock, comprising approximately eight square miles, lies within an area of relatively recent and extensive volcanic activity. Numerous cinder cones, from 200 to 500 feet tall, dot the landscape, and the nearby San Francisco Mountains represent an eroded volcanic cone that formerly loomed about 3,000 feet above its present elevation of 12,670 feet (Figures 1 and 2).

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**Piñon Jay, *Gymnorhinus cyanocephalus*. Painting by Donald Leo Malick.**

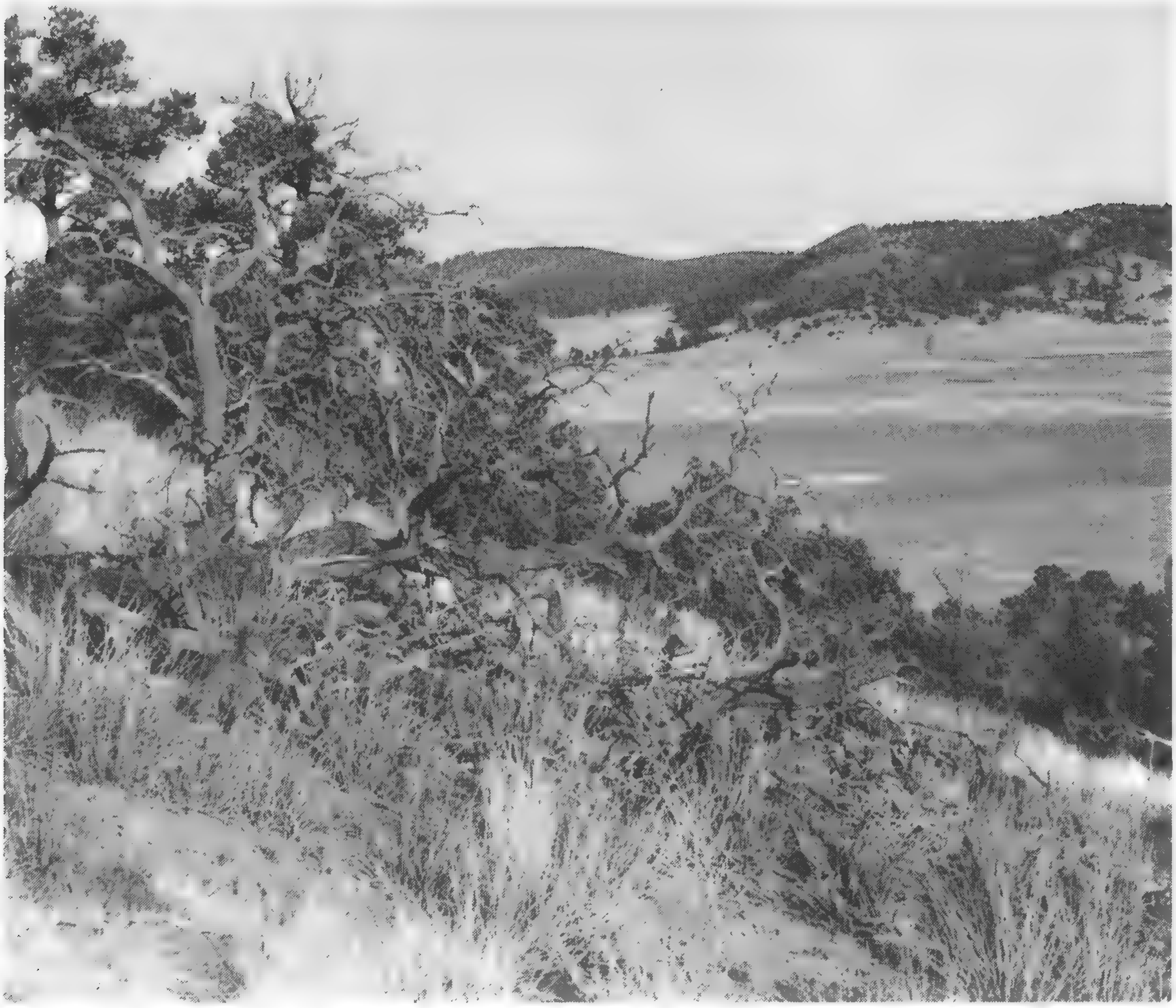

Figure 1. View from a cinder cone on the study area across an open field to other cinder cones. Note the piñon pine trees in foreground.

Within the home range grow three major plant communities, which are, in order of their increasing importance in the year-round activities of the Piñon Jays, old fields, piñon-juniper woodland, and ponderosa pine forest (Balda and Bateman, 1971). The jays spent relatively little time foraging in the open fields during the nesting period.

The piñon-juniper woodland, of *Pinus edulis* and various species of *Juniperus,* occurs primarily on warm south- and east-facing slopes of the cinder cones above the surrounding ponderosa pine forest, a reversal of the usual pattern of elevational zonation of these two community types. Shrubs, more abundant in this community than in any other, include antelope-brush (*Purshia tridentata*), rabbit-brush (*Chrysothamnus* sp.), buck-brush (*Ceanothus fendleri*), and snake-weed (*Gutierrezia sarothrae*). The flock frequented this woodland most often in late summer and early fall when its members harvested the piñon pine seeds, carried them to other parts of the home range, and cached them for later use.

The ponderosa pine forest is the most important plant community within the home range of the Doney Park Flock. The ponderosa pines, of differing ages, are spaced well apart and the canopy is quite open with a well-developed herbaceous layer used extensively by the jays in foraging. A number of shrubs and half-shrubs provide a readily available source of nesting material. Other trees — piñon pine, alligator juniper (*Juniperus deppeana*), Rocky Mountain juniper (*J. scopulorum*), and Gambel oak (*Quercus gambelii*) — comprise less than one per cent of the total forest.

The Doney Park Flock's traditional nesting ground, about 240 acres used at least for the past five years, is within the ponderosa pine community where the trees range in size from small saplings, two to three feet tall, to large mature trees over 120 feet tall ($\bar{x}$ = 32 ft., n = 160).

The area of the Town Flock consists primarily of ponderosa pine community with small portions of fields and woodland and many paved roads along the edges of which the jays feed. The Town Flock also receives heavy subsidies from the year-round feeding stations of local residents.

## *Chronology and Methods of Study*

### Chronology

1968: The birds in the Doney Park Flock started nesting early in March at the same time that timber was being harvested on their traditional breeding grounds. The destruction of many nests and the disturbance to the remaining birds made it impossible for us to determine accurately the time of egg-laying and the nesting success.

1969: We studied the Doney Park Flock before and during the nesting season.

1970: The jays started building nests and laying eggs very early on the traditional breeding grounds. Severe weather conditions with extremely low nighttime temperatures and periodic snowfalls resulted in an extremely low nesting success. The snow destroyed a large number of nests; the adults deserted eggs and nestlings. We saw adult Piñon Jays eating their eggs and young during these adverse periods. Thus we have little data on nesting success and nest placement.

1971: We studied in detail the events prior to and through the nesting of both the Doney Park and Town Flocks.

### Methods

Because the flocks and the individual pairs moved about frequently, it was difficult and often impossible to follow a single color-marked pair for any length of time. Also, because the males and females look very much alike, we could usually identify the sexes only by behavior. The 18 color-marked adults of known sex, observed over a two-year period, helped substantiate our statements regarding the role of each sex in the various behavior patterns. The events described below are a compilation of the behavior patterns of many pairs of birds over a three-year period.

## *Courtship Behavior*

### Silent Food Transfer

This was the first courtship-motivated behavior that appeared in the annual cycle. We first saw it regularly in mid-November every year, and our observations of three banded pairs indicated that this pattern usually involved established pairs and that the males usually fed the females. On three occasions, we saw banded females feeding birds other than their mates.

In the Silent Food Transfer, one bird, having obtained a pine seed or other morsel of food from a cone or the ground or from its throat by regurgitation, held it in the tip of the bill and pointed it at the partner. The recipient took the seed in its bill, flew or walked to a site suitable for opening the seed, and opened and ate it. Sometimes one bird held a seed in the tip of its bill, attracting a second bird, which placed its bill in position to receive the seed, only to have the first bird move the seed back into its mouth. We saw a bird with a seed manipulate it in this fashion as many as four times while the two birds had their bills together.

Food exchange was usually performed within 30 seconds and without vocalizations. At times the recipient bill-wiped after taking the food, and on occasion the provider did the same. Occasionally, a slight quivering of the wings was given by the recipient of the food. During the early phases of courtship, Silent Food Transfer occurred most frequently on the ground and apart from the compact flock.

As the nesting season approached, the jays performed the Silent Food Transfer with increased frequency, more often at greater distances from the feeding flock and off the ground up in the foliage of the trees. After the food transfer, the birds sat quietly in the tree.

Figure 2. A portion of the home range of the Doney Park Flock of Piñon Jays with the San Francisco Peaks in the background.

Gray-plumaged, first-year birds — non-breeders for the most part — also engaged in Silent Food Transfer, but less frequently and without appearing to be selective as to the recipient. One color-marked gray bird fed two other color-marked birds and a third unmarked bird within half an hour.

We have the impression that this display is important in the beginning of pair-formation by first-year birds even though most of them will not breed for another 15 months. In the blue adult birds, we believe that the Silent Food Transfer serves in the formation and strengthening of the pair-bond and may also play a role in reinforcing or establishing the social position of an individual within the flock.

### Courtship Begging

From mid-December on, the jays regularly performed Courtship Begging which also involved the transfer of food, often pine seeds, from male to female. Unlike the Silent Food Transfer, however, Courtship Begging was noisy with a great deal of posturing and loud calling by the female before, while, and after she received the food. This act is reminiscent of begging by juvenile Piñon Jays.

In this display, the female crouched slightly with head and bill pointed upward at a slight angle and the mouth wide open. She fluttered and flapped her partly outstretched wings vigorously (Figure 3) and held her unfanned tail motionless against or near the substrate. Between displays her wings often quivered; sometimes her tail quivered slightly.

Her begging calls, which lasted from three to 34 seconds ($\bar{x} = 18.9$; $n = 106$), consisted of a series of loud "kaws" or "quarrs," vocalizations that became somewhat muffled and distorted during the passing of food. As with the Silent Food Transfer, the intensity and duration of this display increased in the weeks following its first appearance, probably reflecting the physiological readiness to breed.

Early in the season, the jays performed this display most often on the ground and at the periphery of the feeding flock. Later, they commonly displayed up in the foliage and as far as 500 feet from the feeding flock. Females sometimes chased males, performing Courtship Begging on the ground as well as in the foliage. On other occasions, females begged vigorously when males approached with food in the bill — as in Silent Food Transfer. Courtship Begging at the periphery of the feeding flock often preceded a flight by the pair away from the flock and up into a tree.

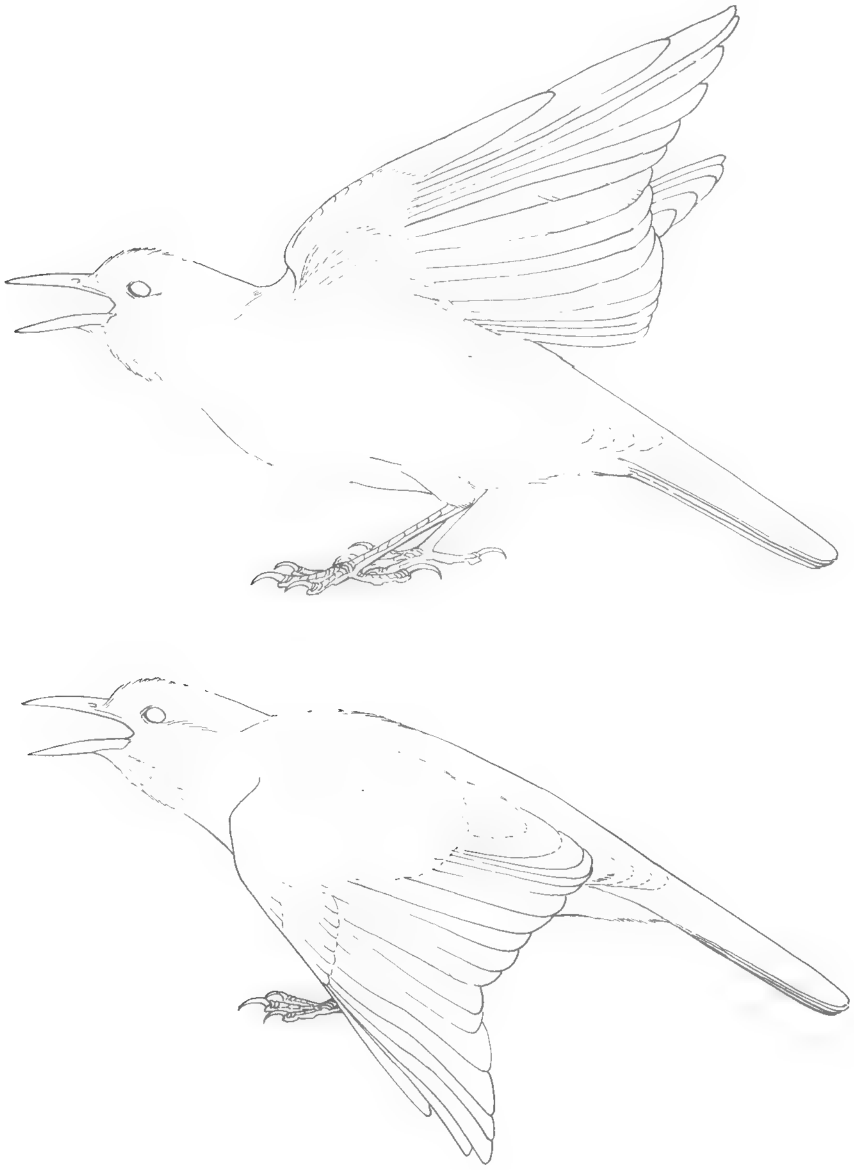

Figure 3. Adult Piñon Jay illustrating postures involved in Courtship Begging.

Gray first-year birds occasionally begged from one another but the duration and intensity of the act were noticeably less than in Courtship Begging performed by adults. The begging did, however, indicate that young Piñon Jays may form pair-bonds early in life.

Courtship Begging is an intricate, ritualized display of key importance in the reproduction of this species. Jays perform it during the incubation period and the early stages of caring for the nestlings when the females spend over 99 per cent of all daylight hours on the nest (n = 68 hours) and are fed almost exclusively by their mates. At one nest, in the spring of 1971, a gray yearling bird helped feed the female. This was the only case of a "helper at the nest" that we observed.

The males fed the females either on or off the nests. When the female was on the nest, the begging display was abbreviated and silent. Since weather conditions at the time of nesting were often inhospitable with nightly low temperatures well below freezing and intermittent snow (Figure 4), and the female's energy demands were high at the very time that she was not able to gather food for herself, it was critical that the male return to the nest site and respond to her solicitations by feeding her.

In addition to the importance of this display in inducing the male to feed his mate during nesting, Courtship Begging may also serve as a submissive display to appease the partner during the early periods of courtship and to appease other members of the flock higher in the social structure. Goodwin (1952) separated a courtship-feeding display from a submissive display in caged European Jays (*Garrulus glandarius*) and found that the former contained definite flaps of the wings while the latter showed wing-quivering. Piñon Jays also performed this submissive display when birds fed in close proximity at a feeding station. The wings were held close to the body and quivered rapidly. Vocalizations may or may not be given. This display is given year round. J. D. Ligon (pers. commun.) has also observed this display in caged birds.

### Silent Sitting

Although this is not a display, we saw it often enough during the prenesting period to include it here. As both feeding displays, described above, increased in frequency, the participants left the vicinity of the feeding flock and perched next to each other in the foliage, near the flock or up to 500 feet from it. During these "silent sittings," pairs performed a number of courtship displays including the Silent Food Transfer.

Flights of pairs away from the flock were often preceded either by a transfer of food — in early courtship — or by the male presenting a twig, piece of grass, or other bit of potential nesting material to the female — in late courtship.

For the most part, members of a pair sat silently next to one another and, on occasion, appeared to sleep. At other times, one of the birds, with feathers slightly ruffled, moved in front of the other while standing upright on the perch. This behavior seems homologous to the "lateral display," described by Goodwin (1952, 1956), and may serve to lower aggression in the mate. Now and then, while the two sat side by side on a branch, one bird turned its head to face the other with its bill pointed directly at the bill of the other bird, which responded in many cases by raising its bill upward at a 50- to 70-degree angle, exposing the white throat patch of flattened feathers (Figure 5). This Chin-up display often ended here. On a few occasions, both members of the

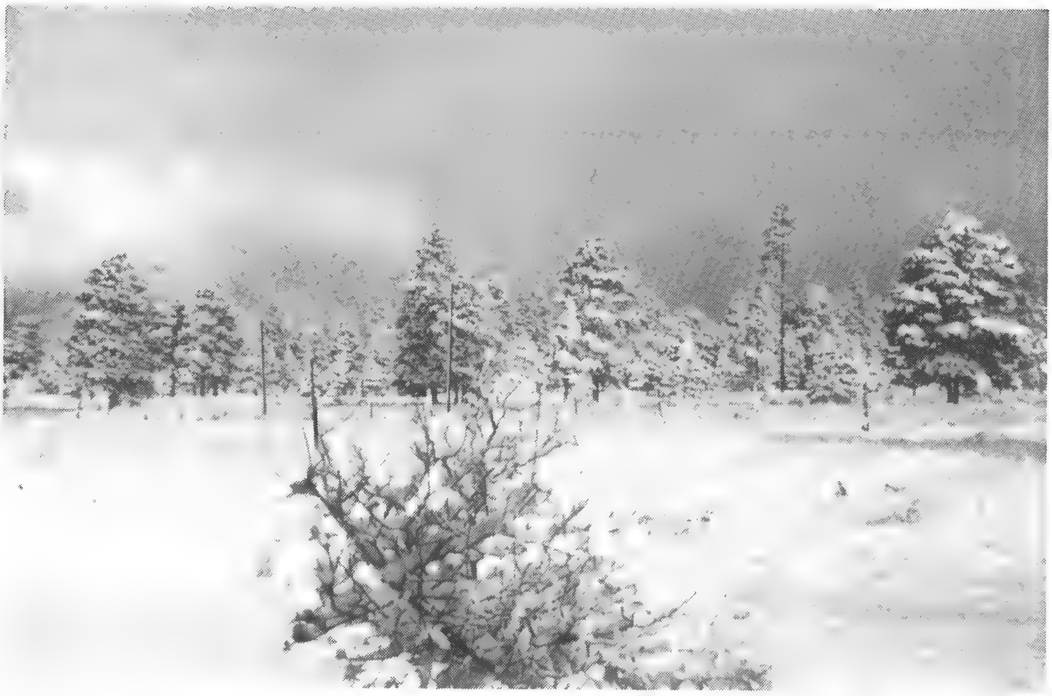

Figure 4. The traditional breeding grounds of Piñon Jays during April 1969 when nests contained eggs and young.

pair alternated with the Chin-up posture. We saw it many times outside the context of courtship and believe it functions in appeasement (Balda and Bateman, 1971).

Another behavior pattern during silent sitting was allopreening — one bird preening another. Sometimes it followed Chin-up, but the jays also performed it independently of any other behavior. The birds most often preened the sides of the head and the nape of the neck with slow, deliberate bill movements. We could not tell whether one sex always performed the preening or whether the preening was mutual. Allopreening also occurred in situations that we would not strictly define as courtship.

The silent sitting periods were occasionally interrupted by soft musical song given by one or both of the pair. The tonal quality of this song, the most musical we ever heard from this species, was very different from the usual calls and sounded to us like a combination of soft whistles, coos, and chirps much like that of a canary (*Serinus* sp.). We heard this song only during the prenesting period from silent sitting through nest construction. It lasted only about 10 to 15 seconds and was not a regular performance.

The jays interrupted the periods of silent sitting occasionally by flying to the ground, foraging together for up to 15 minutes, and then returning to the same perch.

### Stick Manipulation and Courtship Sites

In the later stages of courtship, Stick Manipulation often preceded the flight of a mated pair away from the flock (Figure 6). The jays performed this display most commonly at the periphery of the flock where courtship feedings were also prevalent. In most cases, the male either initiated the display or performed it alone.

When on the ground, the male picked up a stick or piece of grass in his bill and slowly walked up to his mate, presented her with the material, and then flew up into a nearby tree as if to lure her away from the flock. If the female did not respond, he dropped the material and resumed feeding next to her for a short time before selecting another stick. When in a tree, the male simply flew down to the female with the stick in his bill, presented it to her, and then flew up into the tree again. When the female responded, the pair flew off to sit together in the foliage or to engage in other courtship behavior.

The male used twigs and small sticks either picked up from the ground or broken off a shrub, and he often examined three to eight sticks before selecting one to present to his mate. In most cases, he chose twigs of the same material that they would use later in constructing their nest. Hardy (1961) noted that the Blue Jay (*Cyanocitta cristata*) courted only with sticks broken from trees; Gross (1949) and Goodwin (1956) reported that Mexican Jays (*Aphelocoma ultramarina*) and European Jays, respectively, used only freshly broken sticks in their nests.

Stick Manipulation increased in frequency and became more suggestive of nest-building as the courtship period advanced. Sticks and other materials, used by the males to entice the females from the flock, became important vehicles in the displays in the later stages of courtship, during which a male led a female up into the foliage, landed in front of her, placed the stick on a branch between them, and silently fed her. Sometimes the female gave the Courtship Beg at the site and actually chased the male, begging to be fed. After feeding, the male occasionally picked up the stick, moved to a new site, put the stick down between them, and fed the female again. We heard the soft, musical courtship song during these performances. After a varied number of stick-placing plus feeding acts, the pair sat silently together or flew to the ground and resumed foraging.

The pair perhaps then returned to the flock, and after a time the male began searching for vegetation suitable for presentation to the female and enticed her into a tree whereupon they repeated stick placement and courtship feeding. When these displays first appeared each year, individual pairs performed in a number of locations. One pair used four different branches in

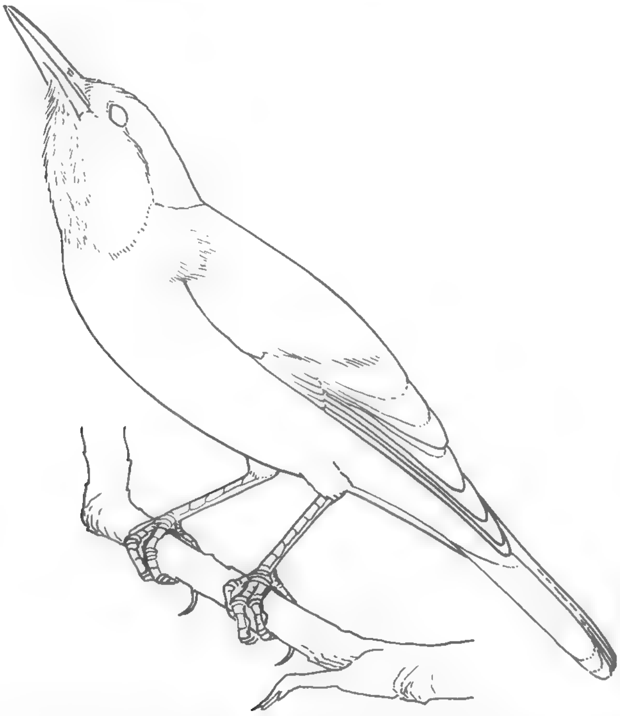

Figure 5. Appeasement posture used by the Piñon Jay. The feathers of the throat region are depressed and the "necklace" is conspicuous.

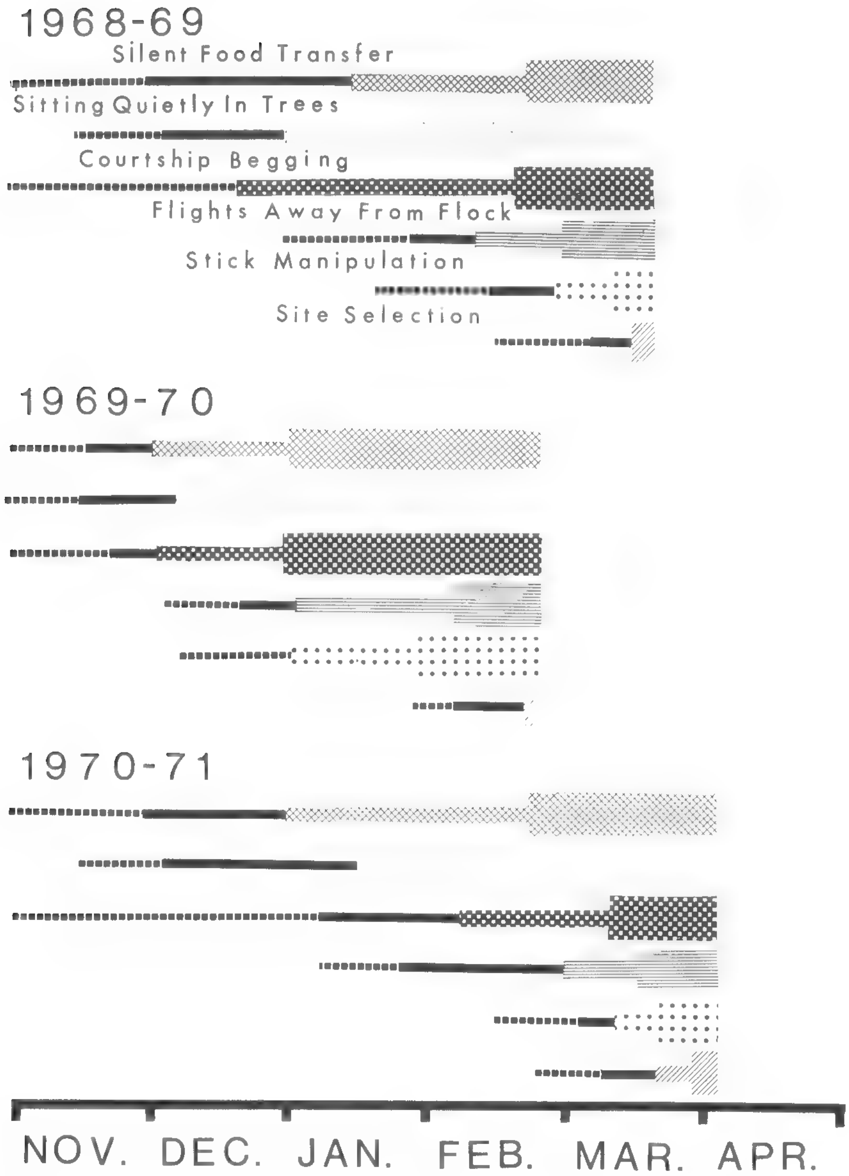

Figure 6. A schematic representation of the temporal sequence of events prior to nesting in the Doney Park Flock of Piñon Jays. The dashed line represents the lowest frequency of each behavior, from three to eight times per hour. The solid line represents moderate frequency, from 9 to 20 times per hour. The narrow bar indicates a frequency of 21 to 30 times per hour, and the broad bar events that occurred more than 30 times per hour.

four different trees in a 45-minute period. Another pair used four different branches in two trees in 30 minutes. The birds performed these displays for up to 10 days before any change in courtship behavior was apparent.

As the time of nest-building approached, the feeding flock began to spend more time on or very near the traditional breeding grounds (Balda and Bateman, 1971). Movements from one area to another decreased in frequency, allowing courting pairs more time for their activities, which — either with or without nesting material — centered on very specific locations that could serve as nest sites.

Usually, a male first attracted a female to a site by carrying a stick to it, entering the site, putting the stick down, and, if she followed, feeding her. Then both birds often examined the site, standing adjacent to the crotch and peering at it intently. One or the other, or both, might try sitting in it. When one bird was in the crotch, the mate usually faced it. Occasionally, the two birds touched bills and Silent Feeding occurred, or the bird outside the crotch preened the nape of the other.

The male sometimes flew to the ground and foraged while the female remained at the courtship site. During these short separations, both birds kept in contact by uttering the soft *kaw-kaw-kaw* call or the *near-er* call. The *near-er,* heard only during courtship and nesting, indicated that the pairs were advancing in courtship from the feeding stage to the use of sticks. After the male found food, he returned to the courtship site and fed the waiting mate. Sometimes she sat in the crotch, and sometimes the crotch was between them. They also performed other acts at the site — "lateral display," allopreening, courtship singing, peering down at the supporting branches — and followed them with bill-raising.

A pair did not select a specific courtship site immediately. Some males spent much longer than others trying to entice a female to come to, and to remain at, a site. Some females came to the sites, took the food presented to them, but did not remain or interact with the males. Other jays often visited pairs that had found suitable courtship sites, evoking a great deal of soft "kawing" and "near-ering." Up to eight birds at once sometimes visited a specific crotch or branch, and birds, other than the resident pair, visited one occupied site 48 different times in two weeks. We saw no conflict at this site.

At a number of other sites, however, the resident pair was very aggressive towards visitors, pecking at them and chasing them off. We observed seven sites with three-bird parties, and the owners never drove the third bird away. In six cases, the third bird stopped associating with the pair; in the seventh, the third bird, a yearling, remained with the mated pair and helped rear the young.

Once a pair selected a courtship crotch or branch, they visited it regularly each time the flock was in the vicinity. We observed four banded birds from four different pairs closely at this period: one pair visited and courtship-displayed in the same crotch 29 times in 16 days; the other three pairs were very faithful to their specific sites.

The sites often held a few sticks, pieces of grass, and small twigs. On four occasions, individuals of a pair brought to their site numerous pieces of plant material, which, after being used in courting, were placed together in what could be described as the very shabby outer layer of a nest. No actual nests resulted, and we believe that this behavior represents an incomplete level of motivation for nest-building or that the birds simply laid the materials at the site after using them to attract the females. Hardy (1961) observed Blue Jays building what he termed "false nests" during the later stages of courtship and early stages of nest-building.

### Courtship Site Selection

During our study period, we located, marked, and observed 61 specific courtship sites, and, using information gathered from over 200 actual nest sites, estimated that 52 (85 per cent) of them could have served as actual nest sites. In addition to being on sturdy branches or in crotches with three to five supporting branches, 54 (89 per cent) were on the southern half of the tree. Only 17 (28 per cent) of the courtship sites ever actually supported nests. Four of these were constructed during the initial nest-building period; the remaining 13 were second nests of the year.

This surprising discovery led us to re-examine the movements of the birds during the late courtship period when the flock spent over 90 per cent of its time in the ponderosa pine forest and up to 40 per cent of each day on, or very near, the traditional nesting grounds (Balda and Bateman, 1971). Instead of selecting areas for observation, we followed the flock for 103.5 hours and observed courtship for 67.5 hours (65 per cent of the total time) on, or just adjacent to, the traditional nesting grounds.

The most intensive courtship seems to occur on both the traditional nesting area and the satellite areas with an emphasis on the latter. Since the satellite areas are not larger than the traditional nesting area, we cannot explain this discrepancy based on the relative sizes of these two areas. The fact that 13 of the 17, or 76 per cent, of the courtship sites actually used for nesting were renestings strengthens our conclusion that most of the intense preliminary courtship occurred off the traditional breeding grounds.

### Nest-site Selection

Nest-site selection, which most pairs performed with maximum frequency for only about four days, spanned the shortest period of any of the courtship activities. This behavior, associated with the selection of a nest site, was closely synchronized between pairs and differed in only a few respects from the selection and use of a courtship site. It occurred on the traditional breeding grounds where all the jays, though they now moved as a flock only during early morning and late evening and sporadically during the day, spent more than 80 per cent of the daylight hours. The jays rarely visited the nest sites of other pairs now, and when they did, the resident pair vigorously drove them off. The male initially chose the site, using sticks and food to entice the female to it. The males and females spent considerably more time at the nest site than they had at the courtship site — thus the integrity of the flock was not pronounced.

At the nest site the males commonly fed the females, and both birds constantly gave low "kaws" and "near-ers." When a pair left the nest site, they frequently fed on the ground nearby and often both returned carrying nest materials — fine grasses and other plant fibers usually used in the lining — and deposited them at, or very near, the site. Most of this material eventually blew away. After three to five days of this behavior, jays began constructing the nest.

### Display Flights

A behavior, very prominent from about the time Stick Manipulation became obvious until shortly before nest-building commenced, was the Display, or Pursuit, Flight. Groups of birds — from two to twelve — flew through and over the trees, performing steep dives and sharp turns and uttering low clucks and low, drawn-out kaws. We saw 85 such flights, 71 of which, or 84 per cent, were performed on, or just adjacent to, the traditional nesting area; all lasted from one to 45 minutes. At times, up to four different groups flew independently. No mixing of individuals was obvious and seldom did the number of individuals change once the flight began.

Although adults performed the majority of these flights, one to three gray yearlings participated in 33 of the 85. Groups pursued banded adult females in six of the flights that usually began with a rapid chase through the branches of a tree. Upon landing, another chase often ensued. At times, chases occurred independently of the Display Flight. As the period of nest-building approached, the number of birds per flight declined; the flights ceased about one week before nest construction commenced. After this time,

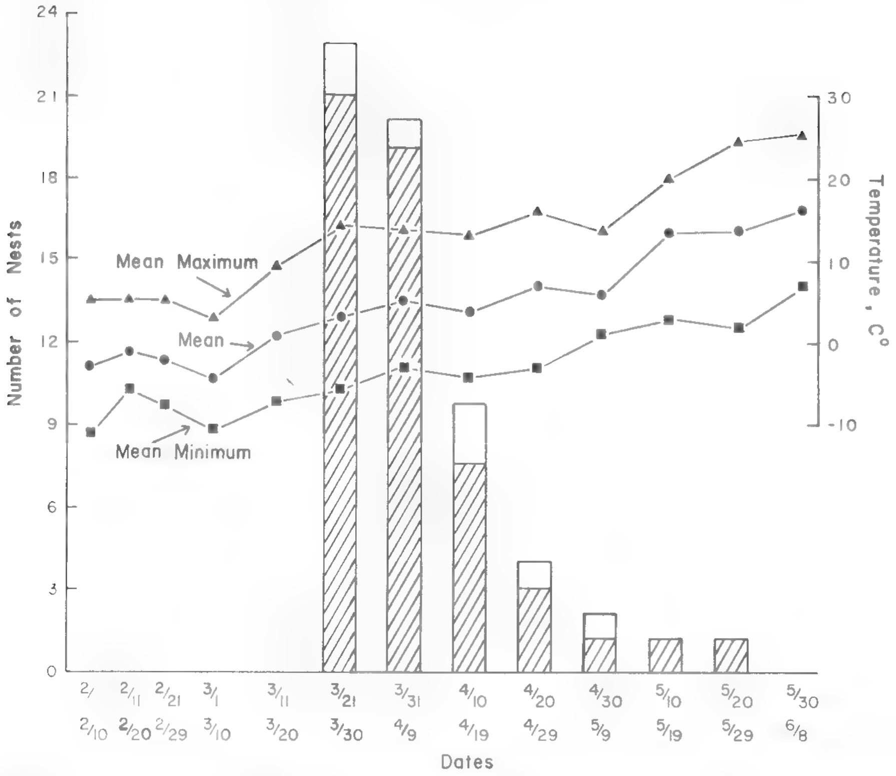

Figure 7. Time of nesting of Piñon Jays and mean temperatures for 1969. Hatched bars are nests known to be initiated within the stated interval. Unshaded portion of bar indicates nests backdated (based on 17-day incubation period).

on rare occasions, we saw groups of from four to eight gray yearlings performing these flights on the traditional breeding grounds.

We believe that these flights consist primarily of unmated males chasing unmated females for the purpose of forming a pair-bond. Goodwin (1951) believed that the somewhat similar "spring gatherings" of European Jays may serve the same function. In the Rook (*Corvus f. frugilegus*), Marshall and Coombs (1957) described similar performances which occur at about the same time in the breeding cycle as they do in the Piñon Jay.

## *Food Supply and Reproduction*

Piñon Jays in northern Arizona begin laying eggs from early March through mid-April when the temperatures are cold and snow not uncommon (Figures 7 and 8), when insect activity is very low, and there is no new plant growth. The ability of the species to nest this early in the year is enhanced by its habit of harvesting pine seeds, produced during the previous late summer and fall, and caching them primarily on, or adjacent to, the traditional nesting grounds.

Piñon Jays harvest and cache seeds of both ponderosa and piñon pines throughout the fall and early winter and use them during all phases of courtship. Both conifers are somewhat sporadic in the production of cones. For example, according to a 10-year study, made in the Fort Valley Experimental Forest 12 miles west of our study area (Larson and Schubert, 1970), ponderosa pines produced 316 cones per acre in 1959, 7,521 cones per acre in 1960, and at least some cones with good seeds every year. Piñon pine seed production is also highly erratic, both temporally and spatially.

Although we have no quantitative data on the production of pine seeds in our area, we recorded qualitative notes each year. Many ponderosa pines had some cones in the autumns of 1969 and 1970, and almost all trees over 40 feet high had many cones in the fall of 1968, a crop rated by G. H. Schubert (pers. commun.) as "heavy." A heavy crop indicates between 3,000 and 6,000 cones per acre (Larson and Schubert, 1970).

In the fall of 1969, the piñon pines on the cinder cones produced a bumper crop with almost every large tree bearing huge numbers of cones containing good seeds, which the jays gathered and cached over a period of at least 22 days. In the fall of 1970, the piñon pines produced only a few cones and most of these contained a high proportion of aborted seeds. The Piñon Jay flock ranged widely and spent little time in the piñon-juniper woodland that fall (Balda and Bateman, 1971). The 1968 crop of piñon pine cones was intermediate to those in 1969 and 1970 (Table 1).

The piñon pine seed ranks second in commercial value to the pecan (*Carya illinoensis*) among the wild nuts of the United States (Fowells, 1965). Each fall the Indians in central Arizona harvest and bring to Flagstaff many pounds of seeds. Information obtained from the local dealer in piñon pine seeds (C. Anderson, pers. commun.) revealed that the variation in seed crops on the study area was consistent with that prevailing over most of northern Arizona. Anderson noted that seed production in 1969 was exceptionally high in the Doney Park area. He also noted that there was essentially no commercial seed crop in 1970.

We have no data on the natural foods of the Town Flock, which was heavily subsidized with sunflower seeds (Balda *et al.*, 1972) from at least four different feeding stations in Flagstaff. Since weather conditions vary only slightly between the home range of the Town Flock and that of the Doney Park Flock, we believe that the additional food affected the nesting cycle of the Town Flock.

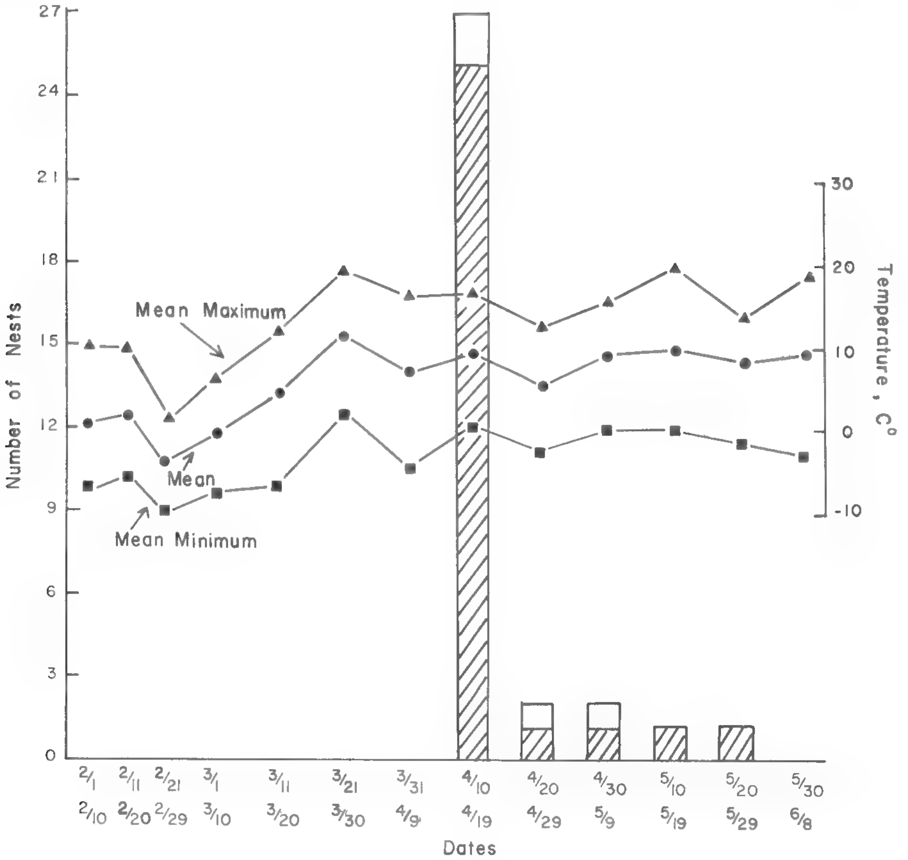

Figure 8. Time of nesting and mean temperatures for the Doney Park Flock in 1971. Hatched bars are nests known to be initiated within the stated interval. Unshaded portion of bar indicates nests back-dated (based on 17-day incubation period).

## *Time of Nesting*

### Temporal Patterns of Courtship Acts

The frequency of the different courtship behavior patterns, based on our observations of the Doney Park Flock and on data obtained only on days when the birds were courting, appear in Figure 6. During and after snowstorms and in exceptionally cold weather, pairs did not court. In 1970, birds courted under colder conditions than in any of the other years; in 1971, conditions were milder than in the preceding two years (Table 2). The Doney Park Flock numbered about 250 birds in 1968, 1969, and 1970; and in the spring of 1971, only 150. We had to adjust our figures for 1971 to make them comparable to other years.

The differences in the intensity and duration of courtship events appear to be directly related to weather conditions and to the varying amounts of food, especially piñon pine seeds, cached by the Piñon Jays the preceding fall.

The two courtship displays that occurred earliest in the season were Silent Food Transfer and Courtship Begging. Both involved food for the female and both continued throughout the courtship period. One of the major roles of both of these displays is probably physiological — to supply additional energy to the female for the formation of eggs.

Silent Food Transfer occurred at moderate and high frequencies for a period of 11 to 12 weeks in all three years, and went on at moderate frequency for much longer in 1969 and 1971. We explain its almost uniform duration in successive years by the fact that it seems to be important psychologically in the formation and strengthening of the pair-bond, appearing early and continuing throughout courtship.

Courtship Begging appeared at moderate and high frequencies for about the same length of time — 11 to 12 weeks — in 1969 and 1970, but declined to seven weeks in 1971. This display probably involves the transfer of larger quantities of food than Silent Food Transfer and leads up to the very similar act of feeding the female during incubation. We believe it to be an important ritual in preparing for nesting duties.

That Courtship Begging functions to supply the female with extra energy seems apparent when we correlate this display with the availability of food and the time of nesting. Following the bumper crop of piñon pine seeds in the fall of 1969, Piñon Jays nested early in 1970. During the fall of 1970, piñon pines produced no seeds and ponderosa pines only a moderate crop, and the birds nested later in 1971 than in the other years.

In 1969 and 1970 at least one type of seed was readily available and the jays performed Courtship Begging at moderate to high frequencies for the same length of time both years. The jays performed Courtship Begging at high frequencies for the longest period in 1970 and for the shortest in 1971. In no year did flights away from the flock and Stick Manipulation reach high frequencies until both feeding events were high.

In years of abundant food, courtship feeding occurred at high frequency earlier in the year. Lack (1966) believed that the food given the female must have survival value or courtship feeding would not have evolved. Earlier, however, he considered such feeding to be simply a courtship ritual (Lack, 1954). Royama (1966) demonstrated that in the Great Tit (*Parus major*) courtship feeding by males may supply the females with one-third of their daily intake of food during the courtship period. We roughly estimate that

## TABLE 1

### Autumn Pine Cone Production and Subsequent Nesting Time of the Piñon Jay

| *Year* | *Cone production* |  | *Mean date of laying of first egg (N)** |
|---|---|---|---|
|  | *Pinus edulis* | *Pinus ponderosa* |  |
| 1968 autumn | Fair | Heavy |  |
| 1969 spring |  |  | 31 March (51) |
| 1969 autumn | Bumper | Poor |  |
| 1970 spring |  |  | 9 March (22) |
| 1970 autumn | Poor | Poor |  |
| 1971 spring |  |  | 15 March (9)T**<br>13 April (29)D** |

*Number of nests in parentheses.
**T = Town Flock; D = Doney Park Flock.

female Piñon Jays receive at least this amount when the pairs perform feeding displays at high frequencies, and thus the females have the energy necessary to form eggs under harsh weather conditions. For many species of birds, nesting success, according to Perrins (1970), is higher for those individuals that nest early in the season. He argued that if courtship feeding allows earlier nesting, then natural selection would favor this behavior.

If a poor winter food supply prevents the birds from nesting early, the relative importance of courtship feeding may be less because during later nestings weather conditions are milder and insects more readily available. The reduction in courtship feeding in 1971 followed a poor cone year and supports this hypothesis. In years of an abundant winter food supply, birds begin courting earlier and court longer probably because of the more inhospitable weather and shorter photoperiod at the time courtship feeding commences.

During incubation, male Piñon Jays supply the females with more than 80 per cent of their food. On many days the females never left the eggs to forage and the males foraged on the traditional nesting grounds to feed themselves and their mates. The time saved in finding and delivering the food to the female can be critical, especially on cold days. Females occasionally, but rarely, left the nest to forage for themselves and returned very quickly. One female fed on piñon pine seeds from a cache less than 50 feet from her nest and was not off the eggs more than three minutes during these forays. In 16 hours of observation, during cold weather with snow on the ground, some incubating females were fed only 3.8 times per day.

It is now possible to propose one reason for courting adjacent to, rather than directly on, the traditional nesting area. The caching of piñon pine seeds in very specific locations each fall has definite advantages for breeding. An ample supply of seeds is made readily available for courtship purposes in one general area and seeds are also available to be used during incubation on another specific area — the traditional nesting area.

### Time of Egg-laying

The availability of food for the brood is certainly a major factor in early nesting (Lack, 1954); however, food requirements of the female must also be considered. We showed that Piñon Jays feed their nestlings a wide variety of insects in addition to piñon pine seeds (Bateman and Balda, in press). In 1970, following a "bumper crop" of piñon pine seeds, the Doney Park Flock nested much earlier than in any other year of the study (Table 1). In 1971, following a failure of the seed crop, they nested much later. The reason that our flock nested at all under these unfavorable conditions, and the flock studied by Ligon (1971) in New Mexico did not, is probably that the large number of ponderosa pines in our area provided an alternate source of food.

Three other lines of evidence support our contention that the time of breeding is related to the fall and winter food supply. First, in years of abundant food, courtship feeding is performed at a higher frequency for a longer period than when food is scarce. Second, although the Town Flock had fewer piñon pine trees within its home range than the Doney Park Flock, at least four feeding stations supplied it generously (Balda *et al.,* 1972). The subsidized Town Flock experienced the same light and weather conditions as the Doney Park Flock, yet the mean date for the laying of the first egg in 1971 was 29 days earlier than that of the Doney Park Flock (Table 1). The food supply seems to be the only logical explanation for this difference. Third, most naturalists agree that in cold, wet springs birds breed late, whereas in warm, balmy springs birds breed early. The Piñon Jay's time of breeding seems, at least partly, unaffected by prevailing weather conditions. The coldest mean temperature and mean maximum temperature for the 15 days preceding laying of the first egg occurred in 1970, the year of the earliest nesting during this study (Table 2). In 1971, the year of the latest nesting, temperatures were mild and no ice and snow lay on the ground for 15 days before the mean date of the laying of the first egg. Thus, we believe that food supply plays a very significant role in determining the time of egg-laying in the Piñon Jay. Perrins (1970) believed this to be generally the case.

TABLE 2

Weather for the 15-day Interval before Egg-laying in Piñon Jays

| *Year* | *Mean tempera-ture** | *Mean maximum tempera-ture** | *Mean minimum tempera-ture** | *Ice and snow* | | *Mean date of first egg* |
|---|---|---|---|---|---|---|
| | | | | *Days* | *Maximum depth*** | |
| 1970 | 36 | 46 | 26 | 9 | 16 | 9 March |
| 1969 | 39 | 57 | 22 | 9 | 32 | 31 March |
| 1971 | 47 | 66 | 26 | 0 | 0 | 13 April |

*Fahrenheit.

**Inches.

## *Clutch Size*

Lack (1966) pointed out that "... while the availability of food might significantly influence the time of laying, it appears to have no significant influence on clutch size." We could find no trend in the mean clutch size from year to year (Table 3) although clutch sizes did vary as much as 0.45 egg in different years. The smallest clutch size, however, occurred in 1971, the year of the latest breeding. Replacement clutches did not show a trend of being smaller than initial clutches. In 1969, first clutches averaged 4.14 eggs and second clutches 4.17 eggs. In 1971, first clutches averaged 3.69 eggs and later clutches 4.00 eggs. This contrasts with our knowledge of many other birds (Lack, 1954, 1966; Perrins, 1970). We believe the lack of a pronounced seasonal variation in clutch size may be due to the availability of different foods at different times of the year. The earlier clutches rely on energy from cached seeds, an exhaustible source and one probably not available for the second nesting. By the time the birds begin renesting, however, insects are more abundant and readily used by females.

## *Nest Materials and Construction*

Piñon Jays build a more or less typical corvid nest — fairly large and bulky (Figure 9) — consisting essentially of two structural components, an outer platform, usually of twigs that serve to anchor it, and an inner cup primarily of shredded grasses. In addition, there is usually a somewhat different layer between the platform and the cup.

The loosely interwoven twigs comprising the outer platform varied in length from 3 to 15 inches. Always well aged, they consisted primarily of Russian thistle (*Salsola kali*), which appeared in all the nests we examined and comprised 50 per cent of the total sticks. Other types of twigs in 20 nests occurred with the following frequency: snake-weed (*Gutierrezia* sp.), 75 per cent; rubber rabbit-brush (*Chysothamnus nauseous*), 80 per cent; tumble mustard (*Sisymbrium altissimum*), 60 per cent; horse-brush (*Tetradymia canescens*), 30 per cent; and groundsel (*Senecio* sp.), 10 per cent. All these shrubby plants grew in the study area, but the Russian thistle was the most abundant and conspicuous with dead plants lying in heaps along fences and next to downed trees where the wind had carried them.

Occasionally, as many as three pairs of jays gathered nesting materials from a single pile of Russian thistles with no obvious interactions between individuals of different pairs. Usually, each member of a pair carried a twig to the nest site. Only four times did we see individuals carrying what appeared to be two sticks at once, and these were relatively short, between four and five inches long. Some larger twigs — one measured 16 inches — were difficult to maneuver to the nest site. The jays carried them crosswise in the bill, and, in one case, when a bird could not get both itself and a long twig through the foliage, it placed the twig atop a clump of pine needles, flew over the clump, picked up the twig, and proceeded to its nest site. If a twig dropped when being placed in the nest, the jay sometimes retrieved it.

In 22 nests, the average number of sticks per platform was 162 ± 14, and the average weight of the platform was 80 ± 5 grams. Although Jensen (1926) found sticks in Piñon Jay nests "as large as a man's finger," the sticks in the nests we examined were almost always less than one centimeter in diameter.

TABLE 3

Timing and Clutch Size in First Nests of the Year in Piñon Jays

| *Year* | *First egg* | | *Range of days in laying* | *Clutch size* | |
|---|---|---|---|---|---|
| | *Mean date* | *Number of nests* | | *Mean* | *Number of nests* |
| 1970 | 9 March | 22 | 8 | 3.95 | 19 |
| 1971* | 15 March | 9 | 5 | 3.88 | 17 |
| 1969 | 31 March | 51 | 17 | 4.14 | 43 |
| 1971** | 13 April | 29 | 12 | 3.69 | 29 |

*Town Flock.

**Doney Park Flock.

After the jays completed the platform, they wove coarsely shredded grasses into the inner twigs. These grasses were difficult to identify because of their condition but we did find *Andropogon, Bouteloua,* and *Poa,* all of which were quite plentiful on the nesting area.

Proceeding toward the center, the grasses in the nest became progressively finer and more shredded. Directly under the cup, there was a layer about one centimeter thick of almost powdery material, which appeared to be finely dissected plant parts. This layer, present in all nests examined, may add significantly to the insulation of the nest.

The nest cup contained a variety of materials in addition to the grasses. Of 20 nests examined, the frequency distribution of items comprising an important portion of the cup was: paper, 95 per cent; rootlets, 85 per cent; pine needles, 80 per cent; feathers, 70 per cent; cotton, 50 per cent; cloth, 45 per cent; and horsehair, 35 per cent. Pine needles and feathers, though present, were not usually abundant in a single nest. Rootlets, on the other hand, often comprised a large part of the inner layer of the cup. The jays often placed pieces of paper, cotton, or cloth directly over the finely shredded material with the cup lining of rootlets built over it. In 22 nests, the nest cup with its lining had a mean weight of 67 ± 6 gm and averaged 46 millimeters thick; the bowls of 43 nests averaged 65 mm deep by 111 mm wide.

Statistical comparisons of nests built early in the 1969 season — before 1 April — with those built later indicated no significant differences in the number of sticks and the weights of platforms or cups.

The time spent in constructing the nest was difficult to measure because pairs curtailed nest-building activities in adverse weather. Also, many nests that appeared to us to be complete had no eggs for some time thereafter. In 1969, no bad weather intervened during nest-building and egg-laying, and we obtained accurate data on 21 nests. The period of building averaged 7.3 days with a range of from five to nine days. The period from the completed nest until the first egg was laid was 2.3 days with a range of from one to five.

Both members of the pair participated about equally in nest construction. Males appeared to do more on the outer portion of the nest where large sticks, as used in courtship, predominated; both carried in the lining. The pairs approached the nest site together and worked together building the nest. Only rarely did we see a single bird working on a nest.

Although nest materials were plentiful near the nest sites, the jays often took materials from each other's nests when these were unattended. If the resident pair was present when another pair arrived, the owners most often called loudly and chased the intruders off. If the intruders refused to leave, actual fights ensued. Birds locked feet and flapped wings vigorously, tumbling to the ground, and sometimes pecked at each other with their bills. This combat was the most aggressive behavior we saw in the entire yearly cycle of the Piñon Jay. In another reaction to intruders, one bird of the resident pair sat in the unfinished nest while its mate attempted to drive them away.

We saw only two nests destroyed by another pair, and in both cases the owners were away from the nest site. In a third case, one pair was delayed about 10 days in completing the nest because of constant pilfering.

Brown (1963) noted that Mexican Jays steal nest materials frequently and that one or both members of a pair defend their nest by sitting on it when a potential robber appears. Piñon Jays behave much more aggressively toward robbers than do Mexican Jays.

## *Nest Sites*

Most reports dealing with the location of Piñon Jay nests come from areas where this species nests in the piñon-juniper woodland. The traditional nesting grounds of the flock we studied, however, contained over 99 per cent ponderosa pine. The trees were spaced well apart and gave the area a park-like appearance. Much of the area surrounding Flagstaff supports ponderosa

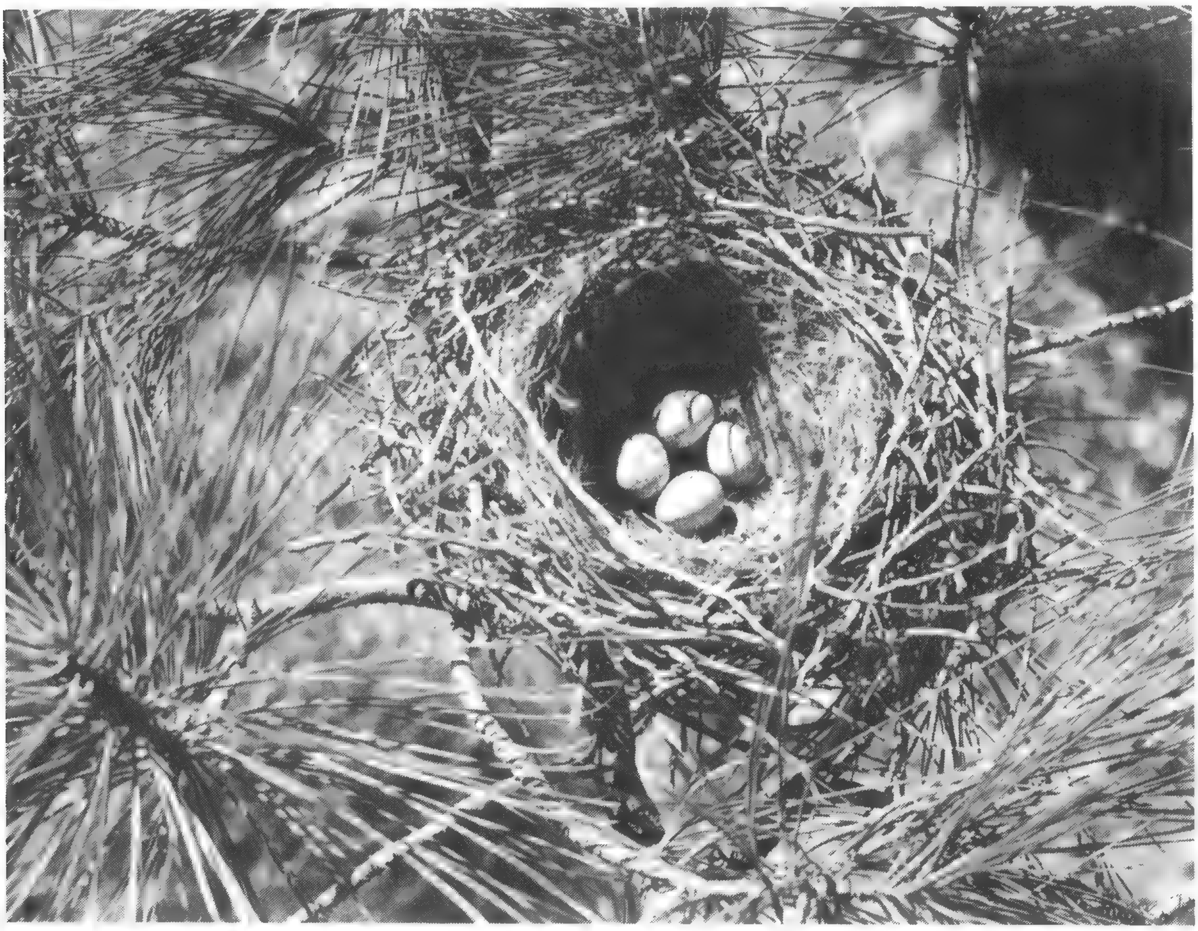

Figure 9. Piñon Jay nest with four eggs. Note the bulky outer layer and thick inner layer of fine grasses and rootlets.

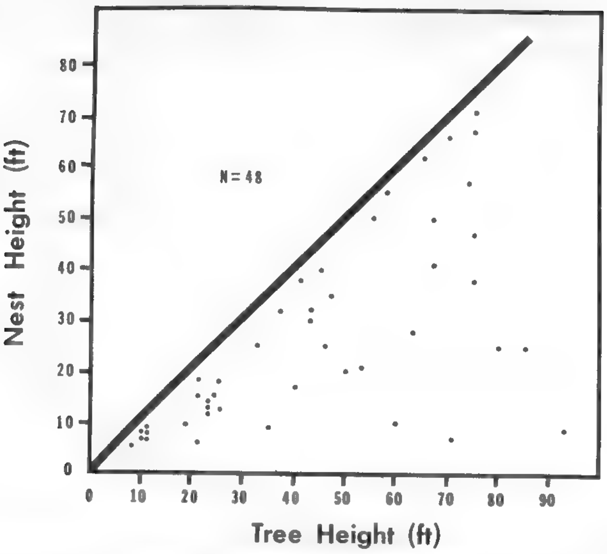

Figure 10. Nest height versus tree height for 48 Piñon Jay nests located in 1968. Black bar indicates maximum possible nest height for trees of a given size.

pine forest; however, in many areas the trees occur in dense thickets and are consequently stunted in their growth. We found no jay colonies in these pine thickets. The openness of the stand may be a factor in the selection of a breeding ground.

MacArthur (1958) showed that large conifers have their foliage divided into zones, with the green needles and buds located at the outer edges of the branches. Only near the tops of the trees are needles scattered throughout the canopy. Ponderosa pines under 35 feet have needles throughout the canopy, similar to the life-form pattern of piñon pines and junipers. In general, one gets the impression that the life-form of the piñon pines and junipers has more green foliage per volume of canopy than does the ponderosa pine. A recent study (Coffman, 1967) has shown that border-grown trees (trees growing in and adjacent to openings) have significantly more (33 per cent) foliage than those grown in closed stands. This difference amounts to 60 square meters of foliar surface per tree. The traditional breeding grounds support ponderosa pines that are somewhat similar in life-form to piñon pines and junipers. Of over 200 nests examined, all but one were located in ponderosa pine.

## Nest Height

Nest height is not correlated directly with tree height. Information in Bent (1946) indicated that Piñon Jays nesting in piñon pines and junipers place their nests rather low, from three to 18 feet from the ground, whereas nests in ponderosa pines are considerably higher. The height of 154 nests, during 1968, 1969, and 1971, ranged from 5.5 feet to 78 feet (Figures 10, 11, 12). The mean heights of the nests were 26 feet in 1968, 24 feet in 1969, and 22 feet in 1971. The differences between years are not statistically significant.

We sampled 160 trees on the traditional breeding grounds and classed them according to height. We also measured the heights of trees that held nests. Heights of nest trees for all years were significantly different ($p < .05$, using the Chi-square test). Figure 13 shows that nest trees were in general somewhat taller than we should expect if the birds selected them solely on the basis of their availability. Since a larger tree has more foliage than a smaller one, it also has more potential nest sites. This may explain the greater number of nest sites in large trees.

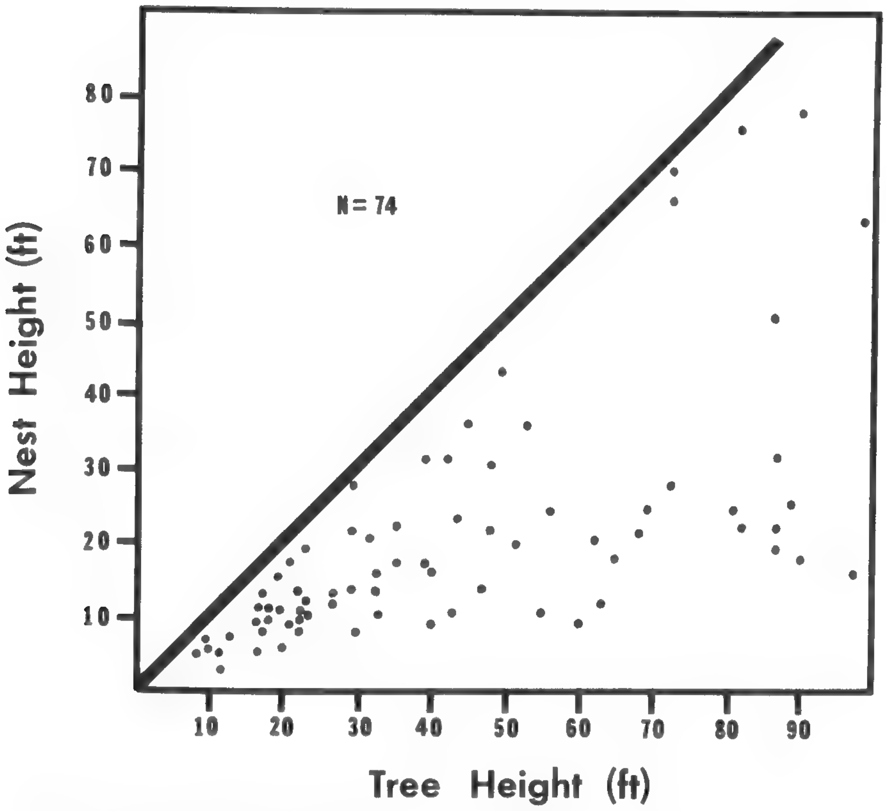

Figure 11. Nest height versus tree height for 74 Piñon Jay nests located in 1969.

### Nest Directions

Piñon Jays consistently placed their nests in the southern half of the tree (Table 4; Figures 14, 15, and 16). This was true in all years of the study. Following Batschelet (1965) regarding statistical treatment of circular distributions, we found that the mean direction of each year's nests deviated less than 20 degrees from due south.

The placing of nests on the south half of the tree may have been due to a variety of environmental factors — uneven distribution of foliage, exposure to the prevailing wind, or the need of solar heat for metabolic maintenance and incubation. We believe we can discount the first two.

Coffman (1967) showed that ponderosa pines growing in the open have 59 per cent of their foliage and branches on the south side. The thickness of the foliage may account for a few of the nests on the south side, but foliage alone cannot account for the high percentage of the nests that occurred there.

Wind direction might conceivably be important. A nest on the lee side of the tree would have less heat loss, less agitation, and less chance of destruction; but data from the weather station at Flagstaff Pulliam Airport for the winter and spring of 1968 revealed that during the nesting season the prevailing wind was from the southwest. During the entire nesting season, the wind blew from the north only 20 per cent of the time, and there was no tendency for the north winds to be colder or faster than the southerly winds. In 1969, a wind-recording station on the study area showed that from early February through May the wind blew from the south 48 per cent of the time and from the north 33 per cent of the time (Table 5). In all the months, the speed of the south wind averaged one mile per hour faster than the north wind, and with winds from the north, the temperatures averaged 1° C cooler in February, 4° C warmer in March, and 3° C cooler in April. Thus, we conclude that Piñon Jays place their nests on the windiest side of the trees.

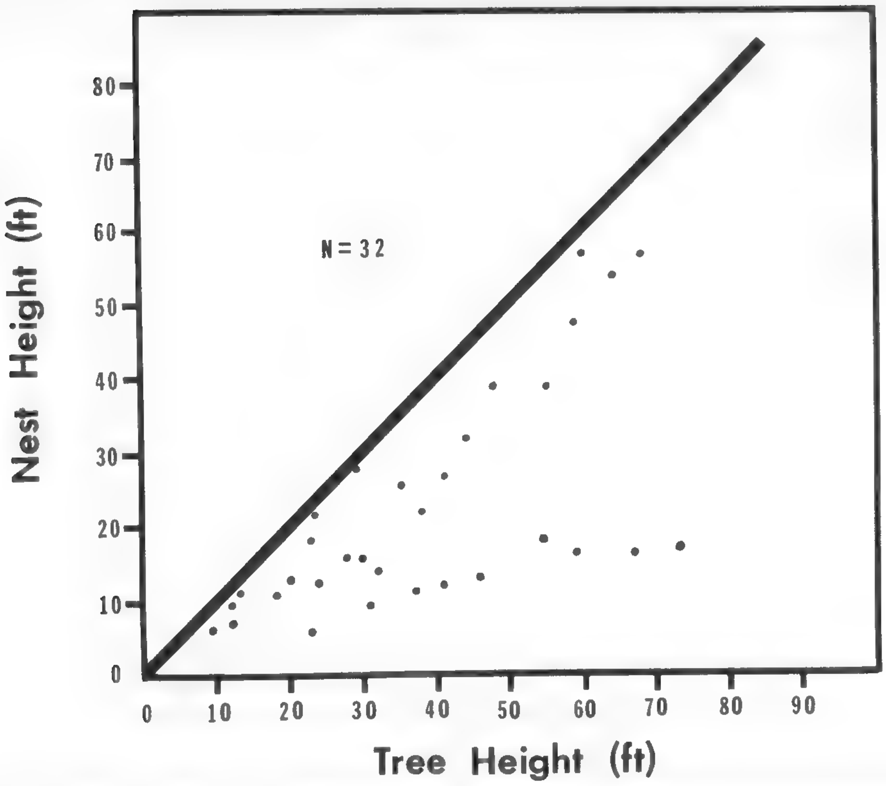

Figure 12. Nest height versus tree height for 32 nests in the Doney Park Flock of Piñon Jays for 1971.

Heat absorption and retention may play major roles in determining the location of the nests. The metabolic saving to a female selecting a nest site in that part of the tree having a slightly warmer temperature may be considerable when the ambient temperature is cool or cold. Although we have not yet completed our studies, we have made some measurements of the temperature differential between opposite sides of the tree. During February, March, and April 1969, we placed a series of black vials around the trunk of a tree and a second series one foot in from the outer tip of the foliage. At hourly intervals, we read the temperatures of the water in the vials (Figure 17). The foliage temperatures averaged 2.3° C warmer on the south side of the tree in February and 2.8° C warmer in March. Temperatures adjacent to the trunk averaged 1.6° C warmer on the south side in February and 1.3° C warmer in March. Figure 17 shows that these differences declined greatly by April. On cloudy days the north-south differential was negligible, and precipitation and heavy low clouds occurred on 14 days in February, 11 days in March, and 8 days in April. On sunny days the differences in temperatures greatly exceeded the means presented here.

If the temperature differential between the north and south sides of the tree is important in energy conservation, one could expect other early nesting species to choose the south sides as well. Unfortunately, little data regarding nest direction are available for other species. Bailey *et al.* (1953) reported that all 19 nests of the Red Crossbill (*Loxia curvirostra*), found in Colorado, were on the south side of the conifers. Kendeigh (1963) showed that nest boxes of the House Wren (*Troglodytes aedon*) in sunlight "... maintain an equilibrium between absorption and loss of heat at a higher level of temperature than in boxes continuously in shade." Consequently, the amount of heat the wren must apply to the eggs is less in boxes in the sun than it is in those in the shade.

## TABLE 4

### Direction of Nests of Piñon Jays from Trunk of Tree

| *Year* | *Number of nests* | *Mean direction** | *Nest concentration*** | *Standard deviation* | *Nest distribution**** |
|---|---|---|---|---|---|
| 1968 | 48 | 186° | 0.736 | 42° | 26.00 |
| 1969 | 73 | 163° | 0.591 | 52° | 24.38 |
| 1971† | 32 | 191° | 0.443 | 60° | 6.28 |
| 1971†† | 18 | 187° | 0.815 | 11° | 11.52 |

*Due south is 180°.

**Intensity of concentration. A value of 1 indicates all nests in exactly the same direction; a value of 0 indicates a uniform distribution.

***Rayleigh Z test (Batschelet, 1965) shows that the distribution of nests was unimodal, with a preferred direction. In all cases, the probability was less than one one-hundreth, $p<0.01$ that nests were uniformily distributed.

†Doney Park Flock.

††Town Flock.

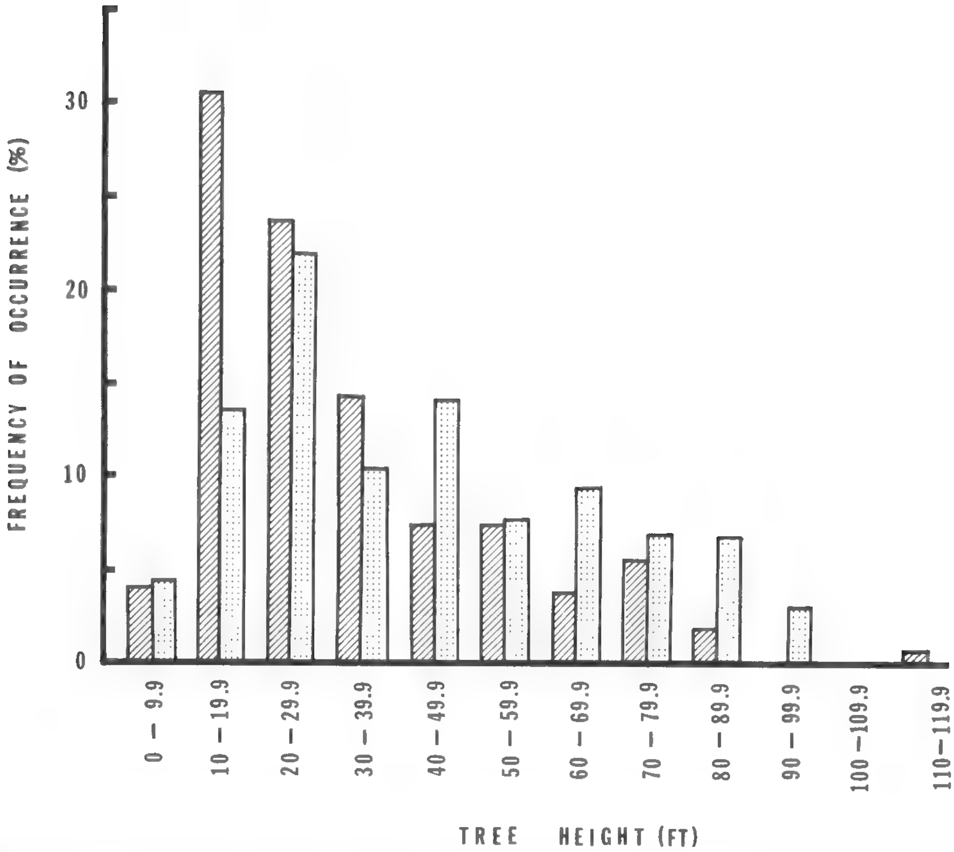

Figure 13. Histogram of the occurrence of trees of various height classes on the traditional breeding grounds of the Piñon Jay. Hatched bars represent a sample of 160 trees. Stippled bars represent the 154 trees used as nest sites.

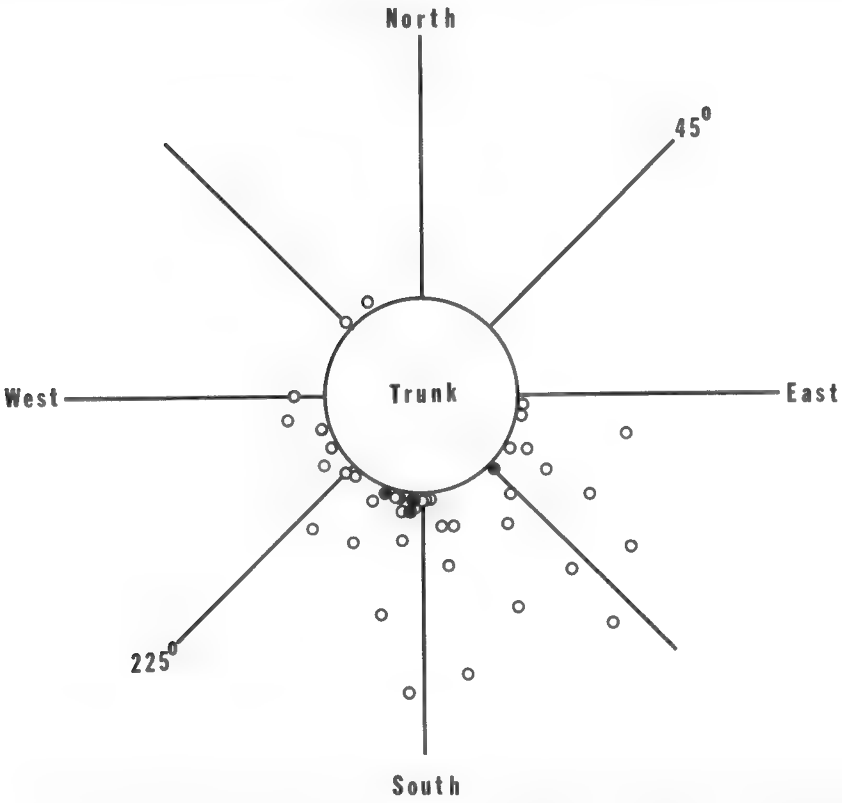

Figure 14. Directional distribution of 48 Piñon Jay nests during 1968. Black dots indicate sites of two or more nests.

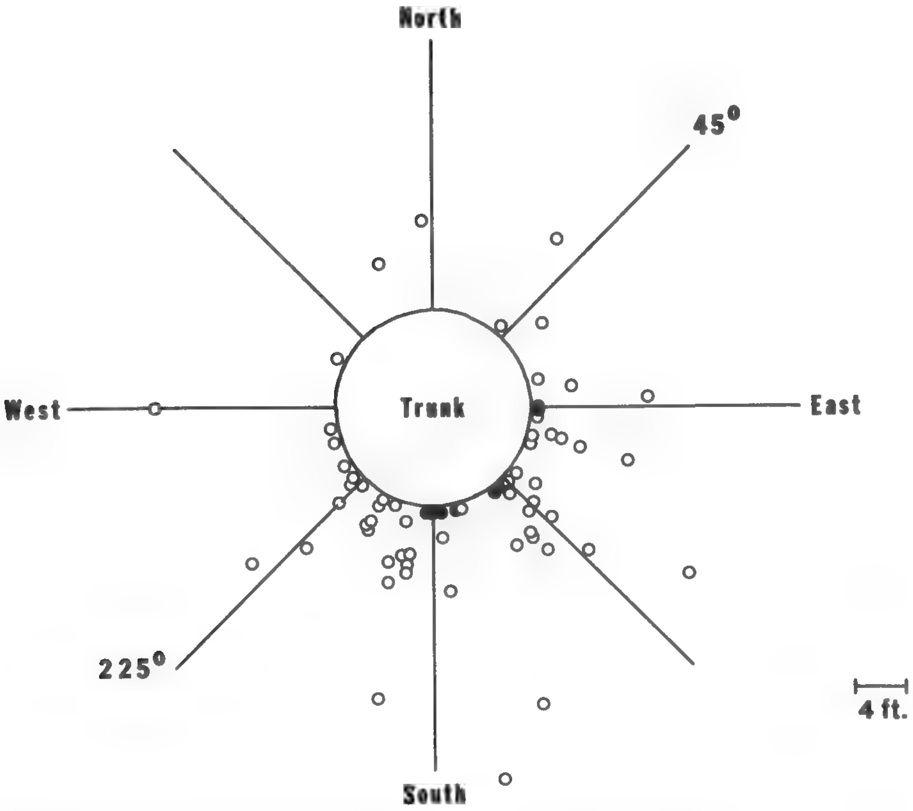

Figure 15. Directional distribution of 73 Piñon Jay nests during 1969.

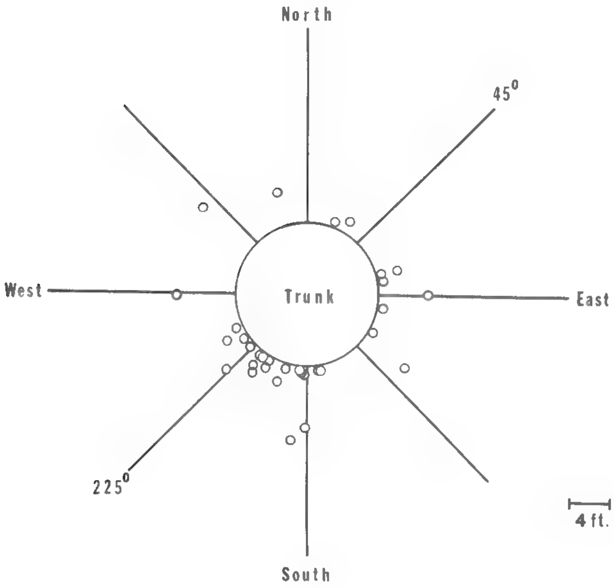

Figure 16. Directional distribution of 32 Piñon Jay nests of the Doney Park Flock during 1971.

If absorption of solar radiation is important during the incubation period, then shifts in the nest placement as the season progresses may be evident and help substantiate our hypothesis. One could expect, for example, that the first nests of the season might be placed on the sunny side of the tree, and that, later in the season, the selection might be more random. Such was not the case with the Piñon Jays; second and third nestings showed approximately the same percentage of nests with a southward orientation.

However, there was one difference. In all years, the majority of first nests were placed out in the foliage (Table 6). In 1968 and 1971, over 80 per cent of the later nests were placed against the trunk. But in 1969, most of the late nests were not against the trunk; they were out in the foliage and just as far out as the earlier nests. A check of the temperatures for the first 30 days of the late nesting period in each of these years showed that they averaged 3° C cooler in 1969 than in 1968 and 1971.

To explain this we must first give our thoughts on why the nests were shifted from foliage to trunk in the late nestings of 1968 and 1971. We believe that early nests are placed out in the foliage because the females need as much heat from the sun as possible when the temperatures range from cool to very cold. Presumably, later nests are placed close to the trunk because the young need shade when temperatures are warmer.

## TABLE 5

Wind Direction in Piñon Jay Colony in 1969*

| *Month* | *North* | *Northeast* | *East* | *Southeast* | *South* | *Southwest* | *West* | *Northwest* |
|---|---|---|---|---|---|---|---|---|
| February | 5.0 | 3.5 | 9.0 | 7.6 | 29.4 | 23.4 | 6.4 | 15.8 |
| March | 15.2 | 7.4 | 4.2 | 4.4 | 10.2 | 19.7 | 16.4 | 22.6 |
| April | 7.9 | 6.2 | 3.9 | 5.0 | 15.4 | 30.7 | 12.0 | 18.8 |
| May | 6.6 | 6.9 | 6.7 | 6.0 | 13.7 | 26.2 | 17.4 | 16.6 |

*Expressed percentage of time.

To substantiate this we turn to knowledge of parental care of the young. The female broods faithfully for about the first seven days — until the skin of the nestlings turns a very dark purple-blue (Bateman and Balda, in press). After that, she leaves the nest more often and for longer periods of time to find food for herself and for the nestlings. The dark-bodied young, exposed to direct sunlight, absorb the sun's heat. One can speculate that the savings in energy gained from a black body is advantageous only up to a point. That is, in nestlings that have not yet gained temperature control, excessive amounts of radiation could cause overheating and, ultimately, death. By April the differences in temperature between the outer foliage and the trunk had largely disappeared, and the nestlings next to the trunk experienced the same warm air as those out in the foliage, without being exposed to the direct rays of the sun. But the colder temperatures in the early part of the late nesting season in 1969 might have influenced the jays to place their nests out in the foliage that particular year.

## *Colonial Nesting*

### Location and Characteristics of the Colony

Ponderosa pines are generally widespread throughout the home range of the Doney Park Flock of Piñon Jays; yet each year the birds began nesting within the same 240-acre tract, the traditional nesting grounds. This area not only supports ponderosa pine forest (Figure 2) but also borders the most centrally located cinder cone, with its growth of piñon pines, within the flock's home range. Each fall, when the piñon pines bear seeds, the jays harvest these seeds and cache large quantities of them on, or adjacent to, their traditional nesting area. This, we believe, is the sole reason for the jays' continual use of this specific area for nesting. Certainly, available nesting habitat within the home range is not found in widely scattered patches, causing the birds to form passive aggregates of nests in favorable habitat, as occurs in some species (Klopfer and Hailman, 1964).

Horn (1968) graphically demonstrated that colonial nesting is selectively advantageous for individual pairs confronted with a clumped food source. Jensen (1926) stated that Piñon Jays in New Mexico "do not return to the same locality to breed year after year. . . ." He observed birds in piñon-juniper woodland with, presumably, widely distributed piñon pines. In woodlands where the food resources are more evenly dispersed over the home range, Piñon Jays may not nest in the same localities in successive years. It it entirely possible that they may not nest in colonies when their food is evenly distributed. Thus, for Piñon Jays, the distribution of food may be very important in determining specifically where they will nest. Lack (1968) correctly proposed that this might be the case.

We mapped all the nests in the colony in 1969 and 1971 (Figures 18 and 19). By overlaying a grid on this map, we determined the coordinates of each nest and calculated the central region, or "centroid," of the colony (after Horn, 1968). Then, taking the distance from the geographical center of the colony to the farthest nest and using this distance as the radius of a circle, we determined the area of the colony.

In 1969, the colony of 54 nests covered 124 acres; in 1971, 32 nests covered only 74 acres. There were some minor shifts from year to year within the 240-acre tract, but in each year the colony averaged one nest per 2.3 acres. This

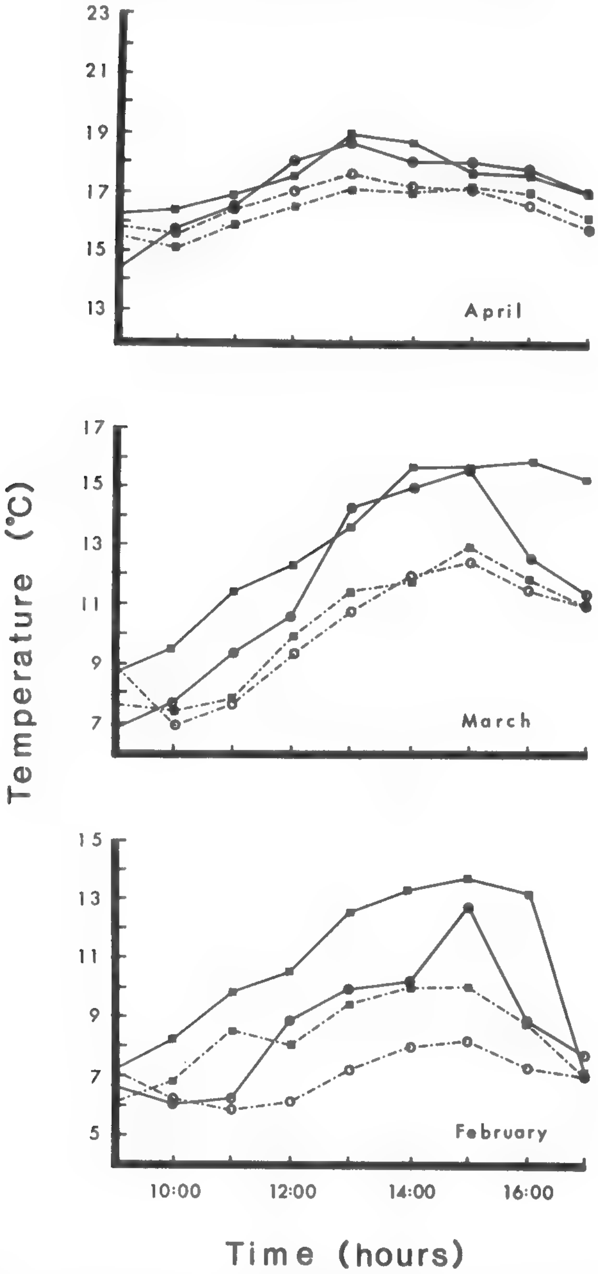

Figure 17. Temperatures on north and south sides of trees in the study area. Solid lines indicate temperatures on the south side; broken lines, temperatures on the north side; squares, temperatures in the foliage; and circles, temperatures on the trunk.

surprising similarity of nest density seemed to indicate some spacing mechanism that should be obvious in the interactions between members of different pairs. Such was not the case. Each pair protected only its own nest and eggs from other jays; otherwise, the birds wandered freely throughout the colony without aggressive conflict.

Using Poisson methods to determine the nature of dispersion within the population, we were able to show a definite clumping effect. The ratio of the variance to the mean was significantly different from 1.0 ($p<0.05$). The mean distance between nearest neighboring nests was 141 feet in 1969 and 126 feet in 1971. In both years, the distance between nests varied from a low of 47 feet to a high of 313 feet. The only two nests in one tree were separated by 54 feet in elevation. Specific nest sites within the colony changed from year to year except in three instances: One crotch held a nest for three consecutive years, and two crotches had nests for two successive years. Unfortunately, none of the birds involved in these three nest sites was banded. All the banded birds selected different nest sites each year.

## TABLE 6

Placement of Piñon Jay Nests in Tree in Relation to Time of Nesting*

| | 1968 | | 1969 | | 1971 | |
|---|---|---|---|---|---|---|
| | *Earliest* | *Later* | *Earliest* | *Later* | *Earliest* | *Later* |
| Total nests | 23 | 25 | 56 | 18 | 26 | 6 |
| Per cent in foliage | 61 | 12 | 61 | 56 | 58 | 17 |
| Per cent on trunk | 39 | 88 | 39 | 44 | 42 | 83 |

*Expressed in percentages of total nests for each period.

### Adaptive Significance

Colonial nesting and its biological ramifications have been discussed at length since the premise of Darling (1938) that individuals within the social group interact with each other just prior to the breeding season in such a manner that gonadal growth in all members is stimulated. If courtship behavior and the associated displays are mutually stimulating, then birds in larger groups will receive more stimulation than those in smaller groups. The outcome of these graded responses should be that in larger groups: (a) nesting is earlier; (b) egg-laying is more closely synchronized; and (c) breeding is more successful (Darling, 1938).

In order to evaluate critically the three hypotheses, we must first establish that there is communication between pairs during courtship and nest-site selection. And here we must rely on our observations. During early courtship, pairs leave the flock and court apart from it. Later, courtship is performed in one general locale by all pairs. Thus, courting pairs are geographically in the same area, performing in a similar manner.

Although courtship sites are usually up in the foliage and partly hidden from view, pairs do visit each other's sites and try to take courtship twigs and sticks from them. Also, all pairs hear the constant "near-ering" calls of others, as well as the loud courtship begging "quarrs." Although we cannot establish the direct results of these displays on other courting birds, there is little doubt that an awareness does exist between pairs during courtship, nest-site selection, and nest-building periods.

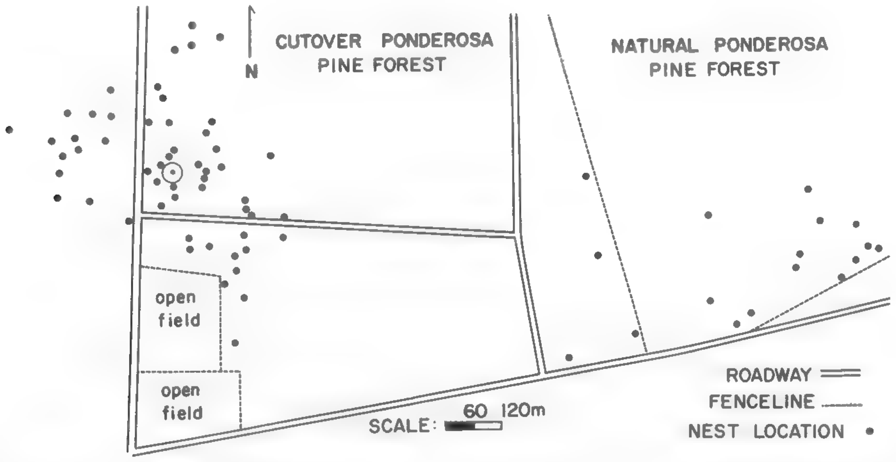

Figure 18. Distribution of nests in 1969 colony of Piñon Jays. Large circle with dot indicates "centroid" of colony. Nests in right half of figure represent a satellite colony.

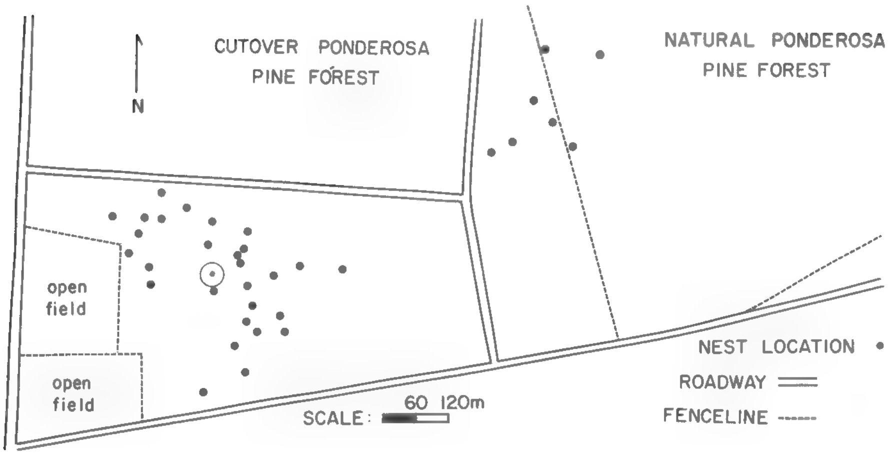

Figure 19. Distribution of nests on traditional breeding grounds of the Piñon Jay colony in 1971. Large circle with dot indicates the "centroid" of the colony. Note smaller contemporary colony in the upper right.

In order to test Darling's three hypotheses within the colony on an annual basis, we looked at the distribution of nests within the colony, using three different approaches:

(a) Having determined the limits of the colony, we divided the area into a center circle and two concentric rings, all equal in area. We then counted the number of nests in each of the three sections and compared the distribution to the expected distribution, using the Chi-square. In each year, the actual and expected distribution of nests differed significantly. Far from being uniformly distributed, we found that the jays placed many more nests in the center circle than in the outer rings (Tables 7 and 8).

(b) We measured the distance from the center of the colony to each nest and then determined the mean distance of the nests from the center. Finally, we divided the nests into those farther from the center than the mean and those closer to the center than the mean. This technique established a circle and a ring within the colony, based on the placement of each nest rather than on the overall area used by the colony.

(c) We measured the distance between nearest neighboring nests and determined the mean distance between nests. We then divided the nests into those with a neighbor closer than the mean distance between nearest neighbors and those with a neighbor farther away than this mean distance.

## Timing of Egg-laying

Assuming that the presence of more birds might result in more intensive social induction of reproductive competence in areas of high nest density, we recorded the time of egg-laying in nests in various parts of the colony. From Tables 7 and 8, one can see that the mean date of laying the first egg was earliest in the central part of the colony in both years, and was progressively later in the more peripheral areas of the colony. The means for both years differed by five or six days from the inner circle to the outer ring.

The mean date of the first egg for those nests closer together than the average distance between nearest neighbors was two days earlier than for nests farther apart than this average (Table 9). Also, nests closer to the center of the colony had eggs earlier than those farther away (Table 10). Thus, pairs with nests in the denser center of the colony and pairs with close neighbors laid the first egg earlier than pairs on the periphery of the colony or pairs with nests spaced farther apart.

Over 90 per cent of the nests in the colony were started within a five-day interval. The average construction time was 7.6 days for nests in the inner circle and 6.9 days in the outer rings, a difference not statistically significant. Because jays rob materials from each other's nests, pairs close together may spend more time defending their nests than do pairs that nest farther apart. Because the pairs in the inner portion of the colony started building two or three days earlier than the others, the difference in construction time is not reflected in the time of laying the first egg.

Once the nests were finished, the birds in the center of the colony waited an average of only 1.6 days before laying the first egg while birds in the outer two rings waited an average of 2.9 days, a significant difference ($p<0.05$). Even if all the nests in the colony were completed on the same day, those in the center of the colony would have eggs before those on the periphery.

The courtship behavior of Piñon Jays involves a great deal of ritual associated with nest-site selection and nest-building. If this behavior is contagious, as Darling (1938) believed, then pairs in a lesser state of reproductive readiness may be stimulated to court by the presence of other courting pairs. One can speculate that if nesting habitat is available adjacent to the areas used by the earlier courting pairs, the stimulated pairs simply nest here. Nests on the periphery of the colony remain eggless for a longer period than do the centrally located nests possibly because social induction — if it operates here — is probably more effective in stimulating the behavioral response of nest-building than the physiological response of egg formation.

## TABLE 7

Fate of Nests in Different Areas of Piñon Jay Colony in 1969*

| | *Inner circle* | *Middle ring* | *Outer ring* |
|---|---|---|---|
| Nests per section** | 30 | 18 | 6 |
| Eggs per nest ($\bar{x}$) | 4.12 | 4.00 | 4.00 |
| Date of first egg ($\bar{x}$) | 28 March† | 31 March | 2 April† |
| Standard deviation of first egg date | 2.61† | 3.93 | 7.89† |
| Wind blown | 4 (14.8)†† | 0 (00.0) | 1 (16.6) |
| Eggs deserted | 5 (18.5) | 4 (26.7) | 2 (33.3) |
| Eggs destroyed by predators | 5 (27.8) | 6 (54.5) | 1 (33.3) |
| Young destroyed by predators | 3 (23.1) | 2 (40.0) | 1 (50.0) |
| Overall nest success | 10 (37.0) | 3 (20.0) | 1 (16.6) |

*Not recorded are nests inadvertently destroyed or used for experimental purposes.

**Statistical significance: $p<0.01$.

†Statistical significance: $p<0.05$.

††Per cent of active nests in parentheses.

TABLE 8

Fate of Nests in Different Areas of Piñon Jay Colony in 1971*

| | *Inner circle* | *Middle ring* | *Outer ring* |
|---|---|---|---|
| Nests per section** | 16 | 8 | 2 |
| Eggs per nest (x) | 3.80 | 3.63 | 4.00 |
| Date of first egg (x) | 13 April** | 15 April | 18 April** |
| Standard deviation of first egg date | 2.28 | 3.45 | — |
| Eggs deserted | 6 (46)† | 3 (38) | 1 (50) |
| Eggs destroyed by predators | 3 (23) | 1 (12) | — |
| Overall nest success | 4 (31) | 4 (50) | 1 (50) |

*Nests inadverently destroyed or used for experimental purposes are not recorded.

**Statistical significance: $p<0.05$.

†Per cent of active nests in parentheses.

Another factor considered was the variability of initiating egg-laying. Horn (1970) showed that this variability increases as the colony size increases in Brewer's Blackbirds (*Euphagus cyanocephalus*). In the Piñon Jays, in 1969 (Table 7), the variability in time of laying the first egg increased from the inner circle to the outer ring of the colony, and the same was true for nests having close neighbors when compared to those having nearest neighbors above the mean distance between nests (Table 9). In all other analyses there was a strong trend toward less synchrony with decreased density of nests, but the trends were not statistically significant. The variability, then, in the date of the laying of the first egg increased as one moved from areas of dense nests to areas of more scattered nests.

## *Discussion*

A critical evaluation of the hypotheses of Darling (1938), the "Darling Effect," has led others to the conclusion that the timing and synchrony of nesting may be due to factors other than intra-group stimulation.

Coulson and White (1956) stated that larger colonies of Black-legged Kittiwakes (*Rissa tridactyla*) had a higher percentage of older birds and bred earlier than smaller colonies. They showed that older birds bred earlier than younger birds (Coulson and White, 1958). Thus, the age structure rather than the social stimuli determined the time of nesting in a colony. Do older Piñon Jays nest more often in the center of the colony than two-year-old birds breeding for the first time? On comparing inner-circle nests to those in the outer two rings, we find that of seven banded adult birds of both sexes, four nested in the inner circle and three in the outer rings. Of the banded two-year-olds, four nested in the inner circle and one in the outer rings. Because so many more nests were in the center than in the outer rings, our data are inconclusive, but they do show that young breeders may nest in the more densely occupied parts of the colony.

## TABLE 9

Fate of Piñon Jays Nests Based on Distances between Nearest Neighboring Nests in 1969 and 1971*

| | *Nests closer than mean distance* | | *Nests farther apart than mean distance* | |
|---|---|---|---|---|
| | 1969 | 1971 | 1969 | 1971 |
| Number of nests | 35 | 15 | 19 | 11 |
| Mean clutch size | 4.10 | 3.80 | 4.00 | 3.80 |
| Mean date of first egg | 29 March | 13 April | 31 March | 15 April |
| Standard deviation of first egg date | 2.53** | 2.06 | 4.27 | 3.83 |
| Nests destroyed by wind | 3 (10)† | – | 2 (11) | – |
| Eggs deserted | 7 (25) | 6 (43) | 4 (25) | 3 (33) |
| Eggs destroyed by predators | 8 (29) | 3 (21) | 4 (25) | 2 (22) |
| Young destroyed by predators | 5 (38)†† | – | 1 (14) | – |
| Overall nest success | 8 (27) | 5 (35) | 6 (38) | 4 (44) |

*Nests inadvertently destroyed or used for experimental purposes are not recorded.

**Statistical significance: $p<0.05$.

†Per cent of active nests in parentheses.

††Statistical significance: $p<0.06$ by Fisher Exact Test.

Social dominance may also play a role in nest selection. J. D. Ligon (pers. commun.) stated that males clearly dominate females. Thus, older dominant males may select nest sites in the center of the colony and the subordinate birds the peripheral locations. This phenomenon might represent a special type of "contagious recruitment" as discussed by Orians (1961). This hypothesis is presently being tested.

Social dominance may also play a major role in determining the time of egg-laying. If dominant birds keep subordinate individuals from some of the food available to the flock, the dominant birds may be in better physical condition and ready to breed earlier. Dominant individuals at feeding stations do repress the subordinate birds (pers. observ.). Thus, the dominance hierarchy may play a role in determining the beginning of egg-laying in highly social birds.

If different individuals experience different habitats, some birds might be ready to lay earlier than others. But with their well-defined home range and gregarious habits, all Piñon Jays within a flock probably experience very similar habitat conditions.

If the microenvironment surrounding the nest sites varies within the colony, then birds at the best sites — presumably the place where the largest groups of birds are located — may breed earlier. We could find no significant difference in the nest sites in different areas of the colony. One could argue that the central area provides some resource not found elsewhere or a greater abundance of resources. Unless resources shift position, we can dismiss this argument because the center of the Piñon Jay colony shifted in 1971 to a site that had been in the peripheral ring in 1969.

Darling (1938) based his hypotheses on observations of gull colonies and because of the myriad of ecological variables involved, as Orians (1961) pointed out, it is extremely difficult to devise a test of these hypotheses for another species. We have demonstrated that, within the Piñon Jay colony, nests are started earlier and with a greater degree of synchrony in areas where nesting density is higher. We have only three examples for comparing nesting times between colonies. In 1971, a small group of pairs from the Doney Park Flock formed a small colony on an area formerly used exclusively for courtship and late nesting attempts (Figure 19). The jays in this colony began their nests at least as early, and possibly up to two days earlier, than the birds in the main colony. The new colony did not show any greater variation in first-egg dates than did the main colony.

In 1971, the Doney Park Flock was much smaller than in previous years and began nesting later. We believe this later nesting was related to scarcity of food rather than to reduced social stimulation.

In the spring of 1971, we found the nesting area of the Town Flock. This flock was about half the size of the Doney Park Flock. We might have predicted that the Town Flock, being smaller, would breed later. Such was not the case. The first eggs were laid by the Town Flock 28 days before the first eggs of the Doney Park Flock, and the mean first-egg date was 29 days earlier. Since both flocks experienced the same weather conditions, we can attribute the early nesting to only one factor — the abundant food provided by the local feeding stations.

### Nesting Success

Orians (1961) discussed the difficulties of relating nesting success to breeding time and synchrony. The factors relating to nest destruction, often very

TABLE 10

Fate of Piñon Jay Nests Based on Their Distances from the Center of the Colony in 1969 and 1971*

| | *Nests closer together than mean distance* | | *Nests farther apart than mean distance* | |
|---|---|---|---|---|
| | 1969 | 1971 | 1969 | 1971 |
| Number of nests | 24 | 13 | 30 | 13 |
| Mean clutch size | 4.08 | 3.83 | 4.29 | 3.69 |
| Mean date of first egg ($\bar{x}$) | 29 March | 13 April | 31 March | 15 April |
| Standard deviation of first egg date | 2.77 | 2.28 | 3.55 | 4.10 |
| Nests destroyed by wind | 4 (18)** | — | 1 (3) | — |
| Eggs deserted | 5 (29) | 5 (45) | 6 (22) | 4 (36) |
| Eggs destroyed by predators | 2 (12) | 3 (27) | 10 (37) | 1 (9) |
| Young destroyed by predators | 2 (22) | — | 4 (36) | — |
| Overall nest success | 7 (31) | 3 (27) | 7 (25) | 5 (55) |

*Nests inadvertently destroyed or used for experimental purposes are not recorded.

**Per cent of active nests in parentheses.

complex, are compounded by man's intrusion. Since the two most important mortality factors — weather conditions and predator density — varied greatly during our study, comparisons of timing of nesting and nesting success between years yield little of interest. For example, in 1970, the Doney Park Flock nested considerably earlier than in any other year and severe weather conditions following nest-building and egg-laying caused the destruction or desertion of just over 80 per cent of the nests. One banded pair renested three times before succeeding in fledging young.

In 1971, the Town Flock nested much earlier than the Doney Park Flock and lost all but one nest because of snow and temperatures 8° C below normal. The Doney Park Flock, which had not started nesting at the time of the storms, was not affected.

In 1969 and 1971, we followed each nest from egg-laying to its end and, using the same three measures as we used for testing Darling's hypotheses, tried to determine whether or not there was a difference in nest mortality within the colony. Overall, the major difference between the two years was due to the intensity of predation. In 1969, predators destroyed 68 per cent of all nests; in 1971, they destroyed 41 per cent. We attributed this difference to the presence of seven Abert's tassel-eared squirrels (*Sciurus aberti*) on the area in 1969 and none in 1971. In 1969, we saw these squirrels eating young jays at a nest, and we collected a squirrel carrying off a banded nestling. Piñon Jays, whether acting alone or as a group, seem to be inefficient in driving away squirrels. Their scoldings and mobbings appear to have little effect.

Patterson (1965) pointed out that the clumping of nests has two possible functions: enhancing the survival of the adults, or providing a net savings in energy used for reproduction. These hypotheses are difficult to test in a Piñon Jay flock because during the earliest nesting — when a colony forms — no pairs nest singly. Clumping of nests is no doubt significant since it allows the males to continue feeding as a flock and return to the nesting grounds as a flock with food for the incubating females and young. This assumes there are definite selective advantages in flocking behavior for Piñon Jays. The scattering of nests in the colony is most likely a compromise between placing the nests close together for cooperative defense against predators and spacing the nests apart so that they are difficult for predators to locate (Kruuk, 1964).

If clumping affords protection, then Piñon Jays' nests in the center of the colony should be safer than those on the periphery. We recorded the number of birds scolding and mobbing us many times. In the center of the colony during the nesting stage, the average number was 4.2 birds ($n = 8$); on the periphery, the average was 2.6 birds ($n = 7$), a significant difference ($p<0.05$). We believe that the intensity of mobbing is greater and scolding lasts longer in the center of the colony.

Because of the differences each year in the number of nests and the predation pressure, we analyzed each year separately. In 1969 (Table 7), the desertion of eggs — as a percentage of active nests — increased from the inner circle outward, as did the loss of eggs to predators.

In 1969, the number of nests with young destroyed by predators increased from the central circle outward (Table 7), and more of the nests with young farther than the mean from the center were destroyed (Table 10). But Table 9 shows that predation on nestlings was greater ($p<0.06$) in nests closer together than the mean distance between nests than in those that were farther apart. Clumped nests may have higher predation during the latter part of the nestling period when the young beg loudly for food, making a commotion sure to attract any predator in the vicinity.

Overall nesting success was higher for nests in the center circle (Table 7). Yet nests farther apart than the mean distance between nests fared better than those closer together. We could interpret this as a compromise in nest dispersion. Nesting in the center of the colony is advantageous because there are more birds to defend the nests; at the same time, having nests well-spaced is also advantageous because a predator must work harder to find each one.

In 1971, the low number of nests in the colony made it difficult to discern significant trends in the data (Tables 8, 9, and 10). Predation was much lower in 1971 than in 1969, and predators destroyed no nests with young. Egg predation was also lower in 1971, more nests being depredated for eggs in the center of the colony than on the periphery. The major egg predators were Steller's Jays (*Cyanocitta stelleri*) and Common Ravens (*Corvus corax*). Steller's Jays, unmolested unless they approached a Piñon Jay nest, had ample time to discover and rob them when the owners were absent. Because of the high egg predation in the center of the colony, the nesting success in 1971 was slightly higher in the peripheral areas (Tables 8 and 10). Thus, we believe that the way the nests are scattered within the colony may be important in nesting success.

## *Summary*

We followed the reproductive and colonial nesting activities of two flocks of Piñon Jays (*Gymnorhinus cyanocephalus*), one for four years and the other for one year, on the breeding grounds in stands of ponderosa pine near Flagstaff, Arizona.

During the courtship activities, which we first noted in mid-November, the jays used the seeds of the ponderosa and piñon pines that grew in the vicinity. Early courtship, complex and highly ritualized, usually occurred when the pair was some distance from the flock. The birds used twigs and sticks in prenesting activities. Courtship feeding occurred often and was probably important in forming the pairs and strengthening the pair-bond as well as in supplying the female with energy needed to form eggs. The female relied upon the male for food during incubation and the early part of the brooding period. The intensity of courtship feeding appeared to be directly related to the supply of pine seeds.

The initiation of nest-building was markedly synchronized. Most birds began construction of their bulky nests in the ponderosa pines on almost the same day and took six or seven days to complete them. Following that, two days usually elapsed before the appearance of the first egg. The jays placed over 85 per cent of all nests ($n = 153$) in the southern half of the tree canopy. Among the possible explanations for this definite directional preference, the metabolic savings to the incubating female of this early nesting species seems to us the most important. Nests built later in the season, when temperatures were higher, were still placed on the southern side of the tree, but more often in shaded sites near the trunk.

Each year the main flock nested in the same area, apparently dependent on it because of the cached stores of pine seeds. Egg-laying began from early March to mid-April in various years and occurred earlier when the previous autumn's cone crop was better.

There was some evidence of social induction, or the influence of others in the group, in the breeding activities. Birds in the center of the colony, where the density of the nests was higher and reproductive activities more pronounced, laid eggs sooner and with more synchrony than the birds near the periphery.

The degree of nest dispersion, or the scattering of the nests within the nesting area, may be a compromise between that spacing which provides protection from predators by adjacent pairs and that spacing that reduces conspicuousness due to clustering. The nests were definitely clustered within the area occupied by the colony and not randomly distributed. It was difficult to correlate breeding success with the placement of the nests within the colony.

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# POLYANDRY IN THE SPOTTED SANDPIPER

HELEN HAYS

Polyandry, as it appears in ornithological literature, is one of those anthropomorphic misnomers which necessitates defining whenever it is used. In humans it literally means that a woman has many husbands at the same time, any one of which could be the father of her children. In birds, a polyandrous female may have many mates, all of which could contribute genes to each clutch of eggs. Until recently there have been no reports in birds of anything approximating this definition. However, Ridpath (1972) discusses breeding trios consisting of a female and two males in the Tasmanian Native Hen (*Tribonyx mortierii*). He recorded both males copulating at least once with the female in most trios.

Jenni and Collier (1972) described polyandry in a population of the American Jacana (*Jacana spinosa*) on a seven-acre pond in Costa Rica. They observed that one female copulated with three different males in a twenty-minute period, and another copulated with four different males in a single afternoon. Molnar (1950) reported more than one male cuckoo copulating with a female.

If the copulations reported in the above instances function in transferring active sperm to the oviduct of the female with ova ready to be fertilized, then several males could copulate successfully with a single female in a matter of minutes, hours, or even days, and the resulting clutch of eggs could be the combined effort of a kind of copulatory roulette. If, on the other hand, the observed copulations do not function in the above sense, the act itself could serve in establishing a bond between individuals, and could or could not help to coordinate their reproductive efforts for a later period when the copula-

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Junior Editor's Note. Many ornithologists have focused in recent years on avian social systems, relating the disciplines of behavior and ecology in their field work. Two such studies appear here. I was excited to learn, when conversing with Helen Hays in November 1971, that in her study of Spotted Sandpipers on Great Gull Island, she had discovered serial polyandry. And I was elated when she consented to submit her work to *The Living Bird,* which she did in March 1972.

Early in the summer of 1972, while teaching at the University of Minnesota's Biological Station at Lake Itasca, I learned of Lewis Oring's work there on the same species — and that he, too, had found serial polyandry among his marked birds. He was acquainted with Miss Hays' study through an abstract she had submitted for a symposium to be given at the forthcoming meeting of the American Ornithologists' Union. I solicited Lewis Oring's paper in July. It seemed appropriate for *The Living Bird* to publish two papers on the mating system of the same species by two ornithologists carrying on independent studies in regions as far apart as Minnesota and New York.

tions would be functional. Although difficult to determine whether or not the copulations are functional, this seems to me a critical point in establishing that these species are polyandrous in the strict definition of the term.

Authors have also used the term polyandry when referring to females of a few families of birds which copulate and pair with a male for a matter of days, lay eggs, and then repeat this pattern with a number of males successively. This is often called serial polyandry.

Finally, the term is also applied in describing behavior of a normally monogamous species in which a female in one season has been noted to nest with two different males.

In rheas (Rheidae) observed in captivity, Steinbacher (1951) mentioned that a number of females mate with one male and all deposit eggs in one nest. The male then incubates; the females move on to another male. In certain species of tinamous (Tinamidae), as in the rheas, groups of females deposit in one nest eggs that only the male incubates. The females then disappear, presumably moving on to another male (Lancaster, 1964). In other tinamous, a single female may mate with a male and then move on to mate with another (Beebe, 1925; Schäfer, 1954). Seth-Smith (1905) noted that his captive tinamou females mated with more than one male. Hauth (1890) and Hoesch (1959), observing captive buttonquail (Turnicidae), noted that females laid eggs for a number of males successively. Hoffman (1949) found that a female Pheasant-tailed Jacana (*Hydrophasianus chirurgus*) might nest with as many as six males in one season. A female paired for a short period with each male, then left him to incubate the eggs while she moved on to the next male. Vernon (1971) mentioned polyandry in the Black Coucal (*Centropus grillii*). Radabaugh (1972), in discussing polygamy in the Kirtland's Warbler (*Dendroica kirtlandii*), noted a single case of successive polyandry. Fraga (1972) reported one case of polyandry in the Bay-winged Cowbird (*Molothrus badius*), usually a monogamous species.

Unbalanced sex ratios in the field have led authors to hypothesize that females of some species nested with more than one male, but no detailed studies of these species are available. Such is the case with the Painted Snipe, *Rostratula benghalensis* (Baker, 1935; Cairns, 1940; Lowe, 1963; Pitman, 1912; Serventy and Whittell, 1962; Whistler, 1949).

In the plovers (Charadriidae), Nethersole-Thompson (1951, 1972, and *in* Bannerman, 1961) reports examples of polyandry in the Dotterel (*Eudromias morinellus*). Polyandry has subsequently been proved in the Dotterel in Austria and Finland.

Several authors have suggested that at least two of the three species of phalaropes (Phalaropodidae) may sometimes be polyandrous but, as pointed out by Höhn (1965), the evidence was indirect and not very convincing. Raner (1972), however, found polyandry in an individually color-banded population of the Northern Phalarope (*Lobipes lobatus*) in Sweden.

In this paper I discuss serial polyandry in a member of the Scolopacidae, the Spotted Sandpiper (*Actitis macularia*), based on the behavior of a small, individually color-banded population of this species that I watched on Great Gull Island, New York (72° 07′ W Long., 41° 12′ N Lat.), during the summers of 1970 and 1971.

Observations reported in the literature (Burger, 1968a; Knowles, 1942; Mousley, 1939; Nelson, 1930; van Rossem, 1925) provide a basis for the hypothesis that the male Spotted Sandpiper does much of the diurnal incubation and brooding. Occasionally, authors reported two birds near nests with eggs or newly hatched young, but the role of the female after the eggs are laid is not described. I, therefore, made a particular effort to follow the females during the breeding season.

The breeding population in both years comprised 17 birds. In 1970, I found six females and 11 males breeding; in 1971, five females and 12 males nested. Most females paired successively with two or more males. Females left the males to incubate as soon as a clutch was complete, with the exception of the final clutch, in which females shared the incubation with the male, but left the care of the young to him.

## *Study Area and Methods*

### Study Area

Great Gull Island lies seven miles east-northeast of Orient Point, New York at the eastern end of Long Island Sound. It is half a mile long and a tenth of a mile wide at its widest point, has an area of 17 acres, and is the site of a large tern colony. Spotted Sandpipers nest in the grassy upland areas of the island.

In 1966, we set up a permanent grid on the island (Cooper *et al.,* 1970), dividing it into quadrats, 25 meters square. Nests mentioned in this paper are located by reference to the grid marker in the northeast corner of the quadrat in which the nest was found (Figures 1 and 2).

### Determining Sex

Female Spotted Sandpipers are slightly larger than males and, in most cases, have more spotting. The first year females, however, are lightly spotted and indistinguishable from males (Theodora Nelson, pers. commun.). Wing measurements of the sexes overlap (Ridgway, 1919). Due to the problem of distinguishing males and females in the field, I determined the sex of the birds, except where noted, by observing copulation in individually marked birds.

### Color Banding

With the help of Donald Cooper and Frederick Schaeffer, I began color banding Spotted Sandpipers in 1967 and 1968. In late May and early June, we mist-netted Spotted Sandpipers in the meadow sections of the island and trapped them on nests. We gave each bird an individual color combination composed of three colored plastic bands and a U. S. Fish and Wildlife Service band. Most of these birds were males.

In 1969, with the help of Grace Donaldson, I tried to trap and individually color mark every Spotted Sandpiper on the island during the last two weeks in May. I felt that by trapping all individuals before they began to nest we could mark enough females so that, in 1970, we could observe any of those that returned. We used treadle traps and funnel traps, baited with maggots from rotting seaweed and set at the tideline on patches of seaweed where small groups of Spotted Sandpipers fed and postured. We also set treadle traps along the paths of the upland sections of the island where the species foraged at high tide. The method worked. Four of the six females, banded in 1969, were back in 1970.

Spotted Sandpipers nesting on the island in 1970 had been color banded a number of years previously: one male, five years before; two males, four;

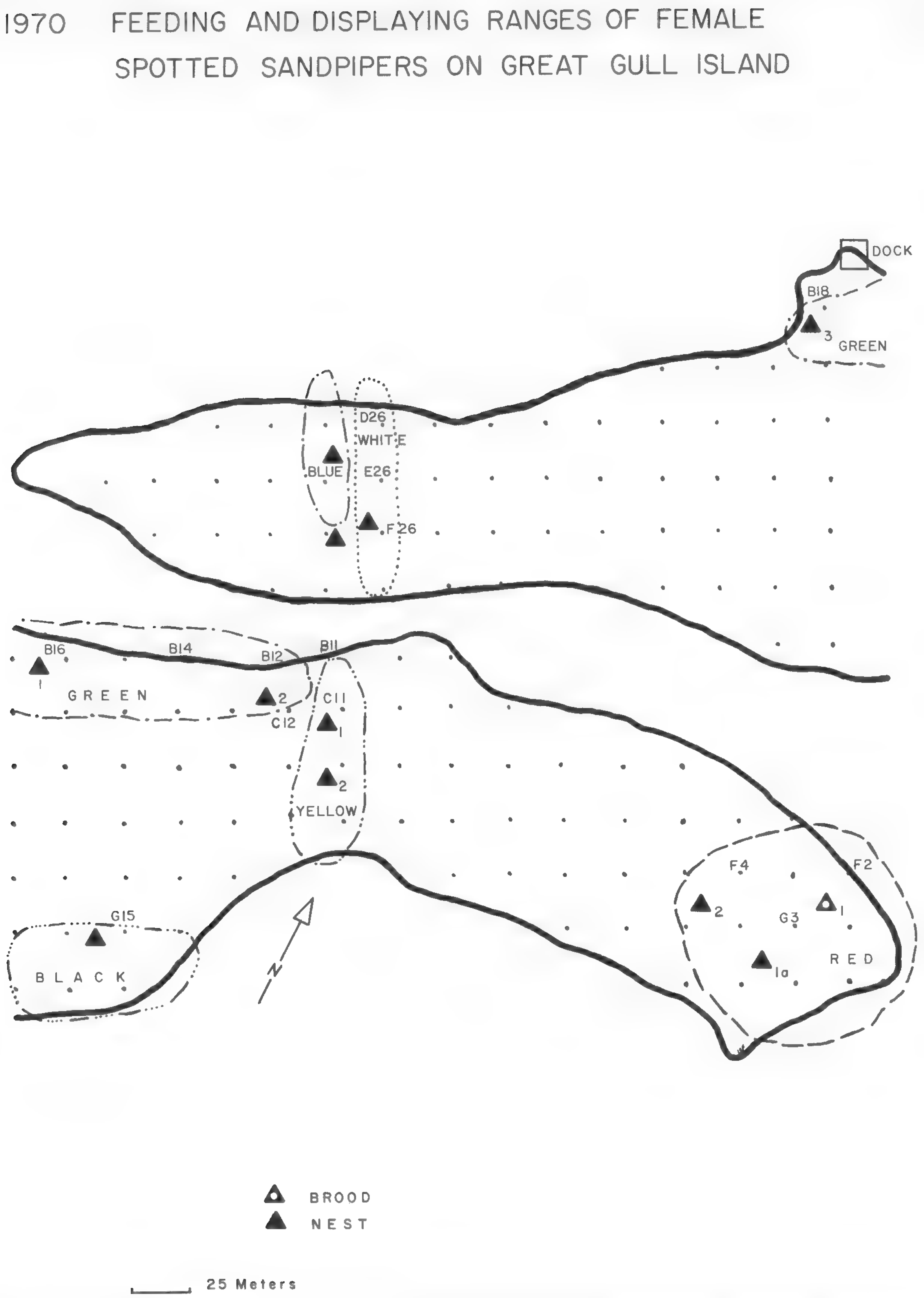
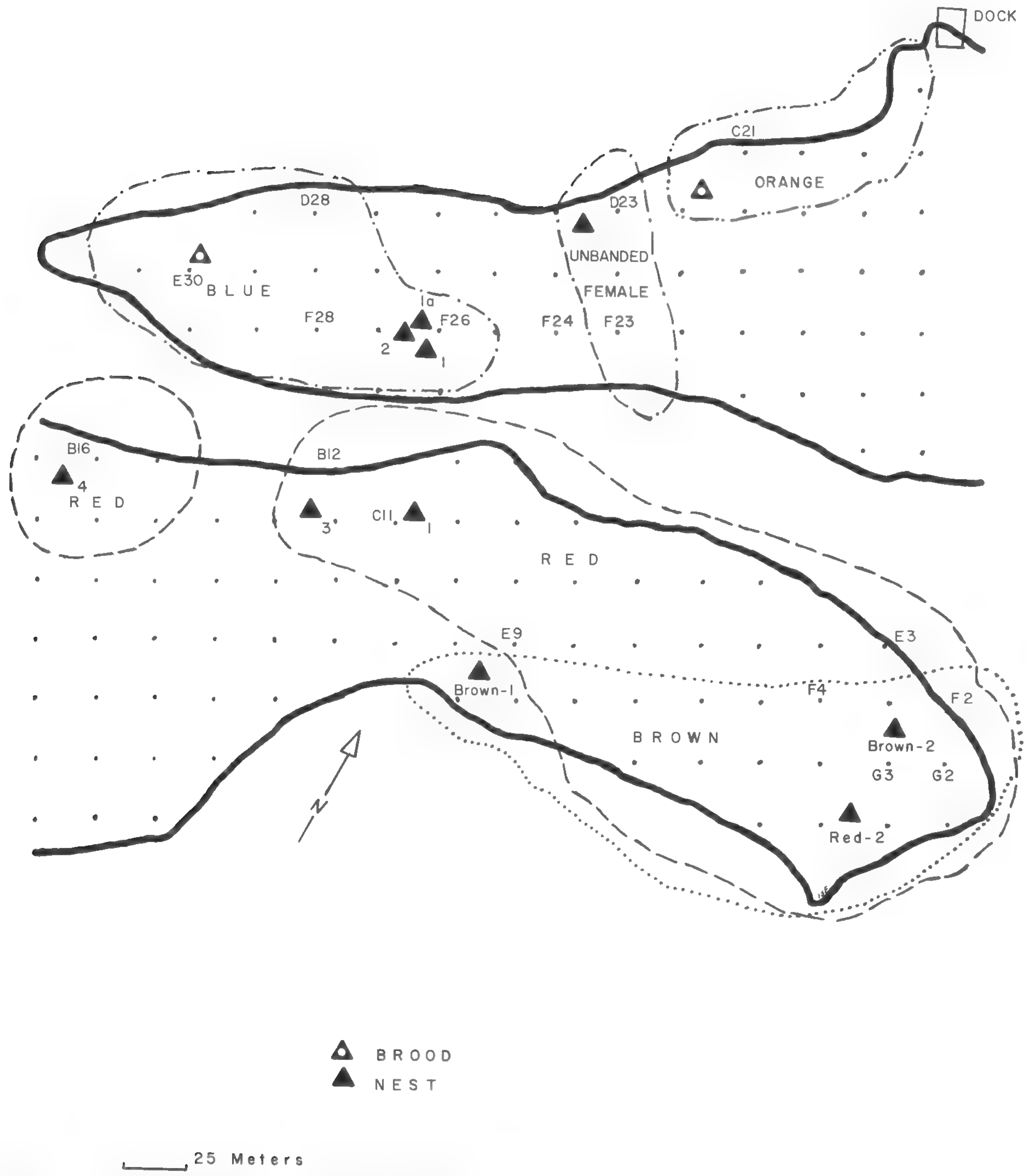

1970 FEEDING AND DISPLAYING RANGES OF FEMALE SPOTTED SANDPIPERS ON GREAT GULL ISLAND
DOCK
B18
3
GREEN
D26
WHITE
BLUE
E26
F26
B16
B14
B12
B11
1
GREEN
2
C11
C12
1
2
YELLOW
G15
BLACK
F4
F2
2
G3
1
RED
1a
N
BROOD
NEST
25 Meters

Figure 1. The feeding and displaying ranges of the six female Spotted Sandpipers that nested on Great Gull Island in 1970. A grid divides the island into quadrats 25 meters square. Grid lines running north-south are numbered 1–30 from east to west. Grid lines running east-west are marked B–G from north to south. Females are identified by a color and their ranges marked with dotted, dashed, or dotted and dashed lines. The nests, broods, or nests and broods of each female are numbered consecutively within her range. Female Red's third nest is numbered 1a because she renested with her first mate after he lost his first brood.



1971 FEEDING AND DISPLAYING RANGES OF FEMALE SPOTTED SANDPIPERS ON GREAT GULL ISLAND

DOCK
C21
ORANGE
D28
D23
UNBANDED
FEMALE
E30
BLUE
1a
F26
F28
2
1
F24
F23
B16
4
RED
B12
C11
3
1
RED
E9
E3
Brown-1
F4
F2
BROWN
Brown-2
G3
G2
Red-2
N
BROOD
NEST
25 Meters

Figure 2. The feeding and displaying ranges of five female Spotted Sandpipers that nested on Great Gull Island in 1971. A grid divides the island into quadrats 25 meters square. Grid lines running north-south are numbered 1–30 from east to west. Grid lines running east-west are marked B–G from north to south. Females are identified by a color or are marked unbanded, and their ranges are marked with a dotted, dashed, or dotted and dashed line. Nests, broods, or nests and broods of each female are numbered consecutively within the range of the female. In the case of female Blue's third nest, it is numbered 1a because she renested with her first male after he lost his first brood. Late in the season we found a brood near grid marker E-30 with no female associated with it. Although it was within Blue's feeding and displaying range, I cannot assign it to her.

three males, three; three males and four females, two; two males and two females, less than one. In 1971, the length of time individuals had been banded stood as follows: one male, six years; two males, five; three males, four; two males, one female, three; one male, one female, two; three females less than one. One male in 1971 is omitted because his partial combination prevented me from determining when he had been banded, and one male was unbanded.

### Daily Observations

In 1970 and 1971, I was able to follow most of the color-banded Spotted Sandpipers from the time they arrived in early May until 10 June. Reading color combinations with a Bausch and Lomb Zoom Balscope, 15 to 60×, I censused the birds daily between 08:00 and 10:00 hours and between 16:00 and 18:00 hours and made additional observations throughout the day. My periods of observation were determined in part by work in the tern colony, the main project during both summers. Regular observations of the Spotted Sandpipers terminated toward the end of May when most of the terns began nesting.

In 1967, Grace Donaldson and I circled the island in a rowboat on the following days: 22, 30 July; 5, 6, 8–11, 19, 20, 26, 27 August; and 2, 3, 9 September. Each day we read bands with Bushnell 9 × 35 binoculars and recorded the color combinations of the Spotted Sandpipers remaining on the island.

## *Results*

### Arrivals

In both 1970 and 1971, I first checked for Spotted Sandpipers on Great Gull Island on 1 May. Females and males arrived at about the same time. In 1970, for example, I saw three banded males and three banded females on 4 May. In 1971, the first banded male arrived on 2 May, three banded males and a female appeared on 8 May, and the last banded birds arrived on 5 June.

### Incubation

I computed the beginning of incubation at 20 days before the hatching date. The literature contains a number of different incubation periods for this species. W. M. Tyler (*in* Bent, 1929) gave 15 days. Burger (1968a) reported 14–18 days; but on recalculating, Burger (1968b) gave a range of 19–21 days. Knowles (1942), Miller and Miller (1948), Mousley (1939), Nelson (1930), and Preston (1951) gave incubation periods for Spotted Sandpipers ranging from 20–24 days.

One clutch that was incomplete when I found it hatched 21 days after the laying of the fourth egg. In 1970, the clutch of one female hatched 26 days after I flushed her first mate from four warm eggs. Only 25–30 meters east of this nest, the same female displayed with her second male. I saw the second male chase the first one on two occasions when the first approached the calling female after he began incubating. The proximity of the female and her second mate to the first nest may have delayed the first male's settling down to steady incubation, resulting in a longer incubation period.

### Nest Histories of Females in 1970 (Table 1)

In 1970, I followed one female, referred to as "Green" because of the color of her band. She nested with three different males successively and the detailed notes on her behavior show the rapidity with which pairs form and dissolve

## TABLE 1

Nest Histories of Spotted Sandpipers on Great Gull Island, 1970

| *Female* | *Male* | *Hatching* | *Evidence for pair-bond* *Copulation* | *Feeding** | *Trapped on nest* | *Flushed from nest* |
|---|---|---|---|---|---|---|
| Green | G-m1** | 13–14 June | 12 May | | | |
| | G-m2 | 19–20 June | | | Female 28 May<br>Male 19 June | |
| | G-m3 | 2 July | | | | Male and female |
| Red | R-m1 | 14 June | | X | | |
| | R-m2 | 30 June | | X | | |
| | R-m1a | 15 July | | X | | |
| Yellow | Y-m1 | 11 June | 15 May | | | |
| | Y-m2 | 19 June | | | Female 15 June | Male |
| White | W-m1 | 13 June | | | | Male and female |
| Blue | B-m1 | 19 June | | X | | |
| Unknown | | 9 June | | | | |
| Unknown | | 2 July | | | | |

*Birds fed together at least 8 days.

**Males designated by mate's color and his position in series of mates. G-m1 indicates the first mate, in 1970, of the female with green color bands.

once the female has completed her clutch. Briefer comments on five other females follow.

I observed Green and her first mate, Green-m1, copulating on 12 May 1970, and flushed Green-m1 from four warm eggs on 18 May.

On 19 May, Green ran along the path behind the dock—D-18—calling. She then flew east to the beach, a short distance from her first nest, and landed on the shore—B-14. In the afternoon, she flew and called near another male, a bird which I had seen daily since 11 May standing on the rocky shoreline—B-11, B-12—and the one that was to be her second mate, G-m2. On 20 May, Green and Green-m2 postured and called along the shoreline east of the dock, and on 21 May, Green-m2 tried unsuccessfully to mount Green.

From 22 through 24 May, between 14:00 and 18:00 hours, I watched the beach area where I had seen the two displaying. On 24 May at 17:00 hours, Green approached a patch of beach pea (*Lathrurus maritimus*). At 17:05 she went into the beach pea and reappeared at 17:23. At 17:28, I asked Grace Donaldson to check the spot where Green emerged; she found one warm egg in a shallow depression. The nest was not checked on 25 May, but at 05:30 on 26 May there were two cool eggs in the nest. On 27 May, between 05:30 and 08:00, I found a third egg in the nest. On 28 May at 05:23, there were still only three eggs, but they were warm for the first time; at 09:30, when I trapped the female on the nest, there were still only three. On 29 May, I found a fourth egg. The clutch was complete.

The day that the fourth egg appeared in Green's second nest, I saw Green running and calling along the path behind the dock. On 2 June, Green and an unbanded bird appeared to be foraging in an area used by Green's first mate for feeding when he came off the nest. On 2 June, between 07:30 and 08:15, I watched Green's first mate, Green-m1, dart toward the unbanded bird accompanying Green. The unbanded bird leapt into the air and landed near Green. With that, Green chased Green-m1 away.

On 8 June, I flushed Green from a nest containing two eggs, and on 11 June, I found four eggs in the nest. Green shared the incubation of her third and last clutch with an unbanded male, G-m3, which I later trapped. For the first three to four days after the clutch was completed, I flushed Green from the nest at different times during the day. From the fifth day until 1 July, the day before the young hatched, I flushed her from the nest only at 05:00 hours. At other times of the day G-m3 flew from the nest. This suggests that, at this nest, the male incubated during the day and the female at night.

Of the other five females that nested on the island in 1970, one female, "Black," was unsuccessful. I found her eggs cold and pecked open. The female "White" nested with only one male; I flushed both birds from the nest throughout the incubation period, and saw both birds with the brood for the first two days after hatching; after that only the male attended the brood. Two other females, "Yellow" and "Red," each nested with two males successively. Red's first mate, R-m1, lost his brood and Red nested with him again. This was the third clutch she produced and the second clutch that her first mate incubated. I trapped the sixth and last female, "Blue," on a nest the day before the eggs hatched. I think that this was her second clutch, but I am not sure because I did not observe her earlier in the season when she might have associated with another male.

### Nest Histories of Females in 1971 (Table 2)

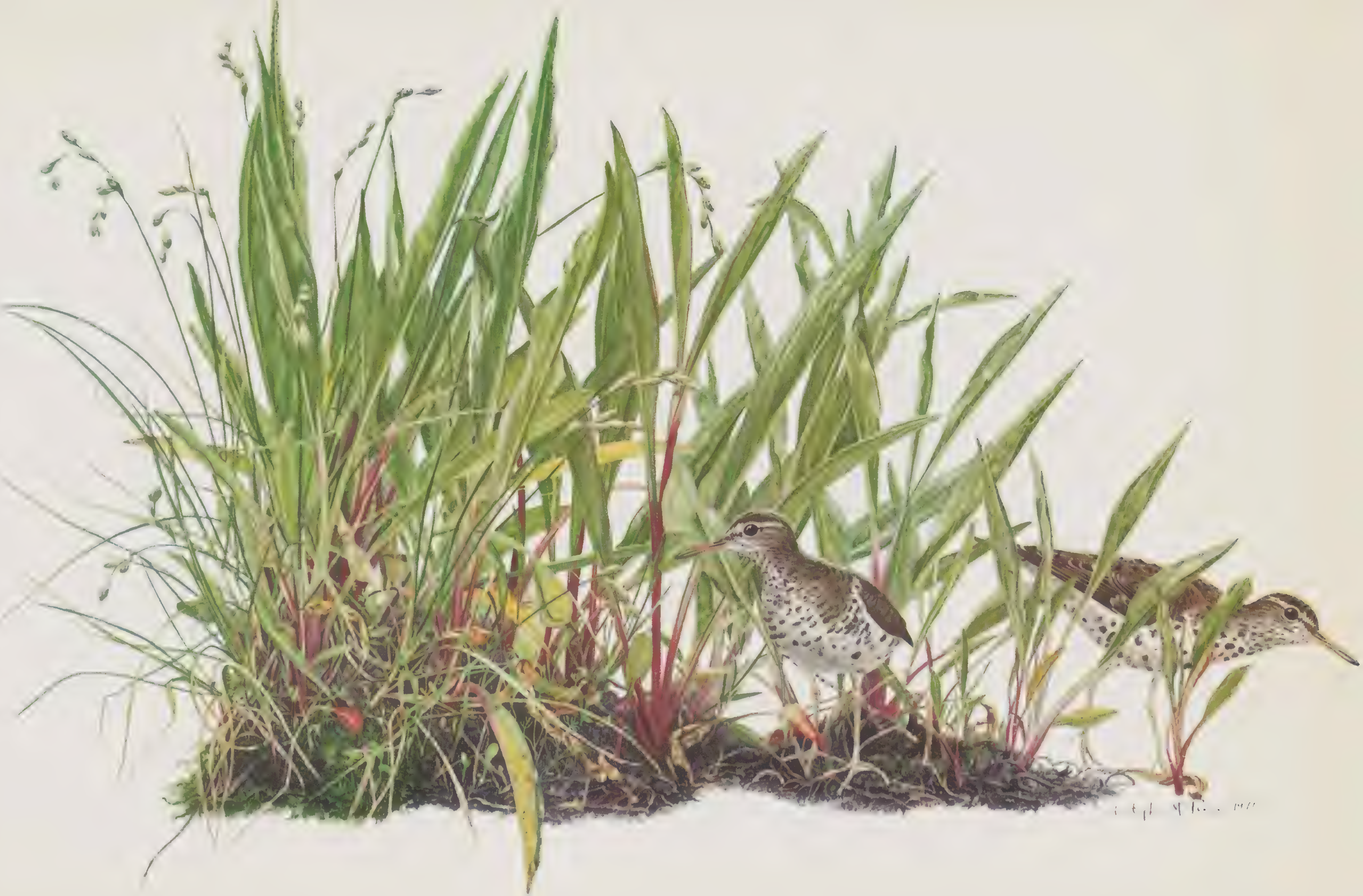
In 1971, only Red and Blue returned to the island. Both completed their first clutches of eggs within eight to 10 days of their arrival. Red paired successively with four males on the eastern half of the island — eight, seven, and seven days apart. Three of these males nested on the island with other females in 1970. The nest sites for each male in both years were remarkably close together, suggesting that males may influence the choice of site. Red's first mate, R-m1, nested in the east meadow — C-10, 11 — and the site of his 1971 nest was only three meters from the 1970 site. Red's third mate, R-m3, incubated a clutch of eggs in 1971 only one meter from his 1970 nest site. Red's fourth and final mate, R-m4, incubated a clutch on the side of a hill, two meters from the spot where he nested in 1970. Red's second mate, also her second mate in 1970, incubated in 1971 at a spot five meters southwest of Red's third nest in 1970.

### Nesting and Feeding Ranges of Red and Blue Contrasted

The feeding and nesting ranges of Red and Blue illustrate the differences in behavior that can exist within a species.

Red nested throughout the eastern half of the island (Figure 2). Her nests were widely spaced, the two closest being some 25 meters apart. During the week that she was with any one male, she spent time feeding both in the area

**Spotted Sandpipers, *Actitis macularia*. Painting by Christopher Pineo.**



where he waited and later incubated, and also at the extreme eastern end of the island.

Blue remained throughout the breeding season at the extreme western end of the island. Her nests were remarkably close together, all three within seven meters of one another. She fed almost exclusively at the western point, occasionally moving east a short distance along the north and south shores, D-28 and F-26. Males fed and displayed with her at the western point. The only time I saw Blue away from the western tip of the island was when she moved 175 meters east and displayed near a male that waited on the shore.

The interactions of Red and Blue with Red's fourth mate, Red-m4, shows the difference in the behavior of the two females. The female that R-m4 paired with in 1970 did not return in 1971. I first saw him in 1971, feeding and displaying near Red and her first mate on the pavement west of the dock, D-19. I then saw Red and R-m1 175 meters east of the dock, C-11, while R-m4 remained near the dock, B-16, calling. Occasionally, he flew to the south shore

TABLE 2

Nest Histories of Spotted Sandpipers on Great Gull Island, 1971

| *Female* | *Male* | *First sighted* | *First banded*[1] | *Hatching* | *Evidence for pair-bond* | | |
|---|---|---|---|---|---|---|---|
| | | | | | *Copulation* | *Feeding*[2] | *Flushed from nest* |
| Red | | 8 May | X | | | | |
| | R-m1[3] | 7 May | X | 11 June | 13, 15 May | | |
| | R-m2 | | X | 19 June | 20 May | | |
| | R-m3 | 15 May | X | 26 June | 2, 3 June | | |
| | R-m4 | 8 May | X | 3 July | | | Male and female |
| Blue | | 10 May | X | | | | |
| | B-m1 | 2 May | X | 12 June | | X | |
| | B-m2 | 15 May | X | 1, 2 July | 4, 7 June | | |
| | B-m1a | | | 12–13 July | | X | |
| Brown | | | 26 May | | | | |
| | Br-m1 | 17 May | X | 25 June | | X | |
| | Br-m2 | 5 June | X | 15 July | | X | |
| Orange | | | 19 May | | | | |
| | O-m1[4] | 21 May | | 5 July[5] | | X | |
| Unbanded[6] | M(F-23) | 14 May | X | 6 July | | | |
| Unknown | M(E-30) | 5 June | X | 23 July[5] | | | |

[1] X indicates bird banded prior to 1971.

[2] Birds fed together at least eight days.

[3] Males designated by mate's color and his position in series of mates. R-m1 indicates the first mate, in 1971, of the female with the red color band.

[4] Unbanded male identifiable by pattern of spotting.

[5] Newly hatched brood; no nest found.

[6] Female unbanded; mate identified by grid location of his area.

on the eastern end of the island, calling, but he always returned to the dock area.

On 17 May, he accompanied an unbanded bird near the dock. On 22 May, I trapped an unbanded bird — judged to be a female on the basis of spotting, wing measurement, and behavior — on the dock and color banded her "Blue-white." R-m4 fed with Blue-white during 22 and 23 May, after which I never saw her again.

From 24 May through 4 June, I observed R-m4 daily at the western end of the island, feeding near Blue. Blue had completed her first clutch of eggs on 22 May, and her future second mate, B-m2, had been feeding on the point near her until 21 May when he too disappeared. R-m4 remained near Blue except for a few occasions when he flew to the area east of the dock. On 28 May, R-m4 mounted Blue but did not attempt copulation.

On 4 June, B-m2 was back on the point at the western end of the island. R-m4 chased him and Blue chased R-m4, whereupon R-m4 left the area. B-m2 copulated with Blue later that morning, and by 10 June he was incubating a clutch of four eggs.

On the morning of 5 June, I saw R-m4 flying and calling over the meadow at the western end of the island. A second bird was present, but I could not see whether it was banded. In the afternoon of 5 June, R-m4 stood on the cistern just east of the dock and below him Red stood on a log (B-16).

During the following week Red and R-m4 fed together and postured. By 12 June, they had begun to share the incubation of Red's fourth and final clutch of eggs for 1971.

Observations of the other Spotted Sandpipers that nested on the island in 1971 are much less complete than those for Red and Blue; their nest histories appear in Table 2. The banded birds, associated with the last three nests to hatch on the island, were seen for one month before they began nesting, contrasting sharply with the rapidity with which Red and Blue completed their first clutches. Orange, for example, paired with an unbanded male and completed her clutch 26 days after I trapped her. I saw the banded males at F-23 and E-30 almost daily for 32 and 27 days, respectively, before they began incubating.

## Aggressive Behavior by Females

Early in the season I watched groups of Spotted Sandpipers chasing one another and posturing. Often the most aggressive birds appeared larger and more spotted, and I guessed they were females. In 1971, I saw several chases by banded birds early in the season in what appeared to me to be two different situations.

In the first instance I saw Red on 8 May, Blue between 15–20 May, and Brown on 5 June posturing with, and sometimes chasing, two banded males. In all but one instance these females later nested with these males. The exception was a one-legged male, one of two that Brown chased on 5 June and with which she fed later in the season. I do not believe they nested. All chases took place at the time the banded birds were first seen on the island, and in areas where the males had nested before. These chases may serve to establish a kind of bond between a female and the several males with which she will eventually pair.

In a second situation of aggressive chasing by a female, I saw a chase that suggested that the female patrolled the entire area where her first three nests were located (Figure 2). On 20 May at 18:30 hours, I watched Red, now paired with her second mate, fly across the meadow from the south side of the island, E-9, to the north side, B-10, and land on the path near her first nest. She chased an unbanded bird, which I judged on the basis of size, spotting, and behavior to be a female, along the path. The unbanded female had been posturing near the male which was to become Red's third mate. The future R-m3, as well as R-m1, joined her in the chase. At that moment, a person walked through the meadow, but, before the birds scattered, I had the impression that Red was chasing the unbanded female out of the area. The observation suggests that females, by patrolling and defending large areas, keep potential mates isolated.

### Posthatching

In late July and August of 1967, we checked Spotted Sandpipers to determine how long the adults and young remain on the island. No adults from nests that hatched in June were present. One male, from a nest that hatched on 4 July, defended the nest site through 30 July. A female from a nest that hatched 16 July had molted and had lost the spotting on her breast by 8 August. She remained through 20 August.

Of the 34 young Spotted Sandpipers, banded on the island in 1967, we recorded 10 later in the season when they were no longer associated with an adult: two up to four weeks after hatching; two up to five weeks after hatching; three up to six weeks after hatching; and three up to eight weeks after hatching. We saw many of these birds between 22 July and 20 August on more than one day, some on as many as eight days. In all but one instance, the birds foraged along the shore near their hatching sites, seeming to remain within limited sections of the shoreline, and some defended these areas against others of their species.

## Discussion

My observations of females Orange, Red, and Blue, as well as their mates, suggest that birds returning to the island nest more quickly than birds coming to the island for the first time. Red and Blue, females that had nested on the island before, completed their first clutches within eight days of their arrival; Orange took 27 days after I banded her to complete her clutch.

The nest histories of Red and Blue suggest that the association of the male with a particular site and the female with a larger area that includes a number of sites may be more critical for rapid pairing than the bond between any particular male and female. The three males that nested for the first time with Red in 1971 nested at almost the same sites in 1970, but with different females. At times, however, the attachment to a site may inhibit pairing away from that site. Thus, the attachment of female Blue and male R-m4 to different areas may have prevented them from pairing with one another. And the attachment of R-m4, as well as the male at F-23, to sites that did not fall within the range of a territorial female, appeared to isolate them, which might function to delay pairing.

A lessening of importance of the pair-bond and the increasing importance of attachment of individuals to particular sites or areas could serve as an adaptation facilitating the development of serial polyandry as is seen in the Spotted Sandpiper, as well as polygyny in other species.

The variability in pairing behavior of female Spotted Sandpipers suggests that this species still may be evolving its polyandrous form of nesting behavior.

Females nest with different numbers of males. White, in 1970, nested with only one male and shared the incubation of the clutch with him. Most of the other females, however, did not incubate until their second, third, or fourth clutch. It is evident that since a number of males incubated and took care of the young without the female's help, her assistance in parental care is not necessary for successful reproduction. That she sometimes does so suggests that a tendency to incubate still exists.

In the Scolopacidae, there is a widespread tendency for reversal of sexual roles, and, in quite a few species, males take over much of the incubation and care of the young. In most of the latter instances, the females tend to be larger and occasionally differ in color with the most extreme examples in the related phalaropes and the painted snipes.

In discussing sexual dimorphism, Amadon (1959) began with Darwin's theory that competition for mates results in one sex, usually the male, being larger than the other. Amadon also noted that in some groups, such as the shorebirds, the females may be larger and more brightly colored because they compete for mates.

Selander (1966) discussed sexual dimorphism in certain species as an adaptation to different niches. Pitelka (1950), when reporting on sexual dimorphism in the Long-billed Dowitcher (*Limnodromus scolopaceus*), in which the female is larger and longer billed than the male, suggested that the female's longer bill gives her an advantage by enabling her to feed in deeper water. On Great Gull Island I can see no difference in feeding areas between the male and female Spotted Sandpiper, and I assume that both sexes eat the same organisms where they do feed, as would be expected, since their bills are about the same length (Ridgway, 1919). The tendency toward sexual dimorphism in this species, from my observations thus far of birds on the breeding ground, suggests competition for mates rather than an adaptation of the sexes to different niches as the selective force influencing sexual dimorphism.

Mayr (1939) suggested that the primary and secondary sex ratios of certain species may be unequal, creating an imbalance in the tertiary sex ratio. Orians (1961) suggested that primary and secondary sex ratios of Red-winged Blackbirds (*Agelaius phoeniceus*) are equal, but that ecological factors have caused the delayed maturation of males, thus creating an imbalance in the tertiary sex ratio.

The primary and secondary sex ratios for the Spotted Sandpiper are not known. The multiple clutches of the females, however, may result in an imbalance of sexes in favor of the males. On the basis of the limited numbers of birds in two years, proportionately more males than females returned to nest in 1971. If, in the course of future observations, this difference is shown to be more than fortuitous, it might suggest that multiple clutches is a factor producing an imbalance in the tertiary sex ratio.

Within the Scolopacidae there is a tremendous variation in sexual behavior. The promiscuous Ruff (*Philomachus pugnax*) and polyandrous Spotted Sandpiper exemplify two extreme forms of behavior. Interestingly, both of these forms are characterized by sexual dimorphism, an imbalance in the tertiary sex ratios, and a strong attachment by the males to particular areas. In the Ruff a number of males remain, when courting, in very restricted areas and the females come to the males in these areas to mate. In the Spotted Sandpiper the males become attached to particular nest sites. The females may defend areas that include a number of sites or move freely from one site to another following the completion of a clutch.

With the decrease in importance of the pair-bond and an increase in attachment to particular areas, polyandry, polygyny, or promiscuity develops. Determining the factors that influence this development is perhaps not possible, but a closer look at behavior in some of the monogamous members of this group might prove useful. In Temminck's Stint (*Calidris temminckii*), Hilden (1965) reported that the female regularly lays two clutches of eggs; the male incubates the first; the female the second. Parmelee (1970) suggested a similar pattern for the Sanderling (*Crocethia alba*). The production of multiple clutches, as well as the reversal of sexual roles, may represent behavioral and physiological adaptations essential for the evolution of polyandry. The behavior of other forms, not yet described, may prove to represent intermediate behavioral stages from which polygynous forms of behavior have evolved. The Scolopacidae, more than any other family, offers an excellent opportunity to learn about the development of polygynous, polyandrous, and promiscuous forms of sexual behavior.

## *Summary*

During May and June of 1970 and 1971, I observed an individually marked population of Spotted Sandpipers (*Actitis macularia*), comprising 17 birds on Great Gull Island, New York. Females often nested with a number of males successively.

In 1970, six females initiated 12 nests. The females nested with males as follows: two were monogamous; two females each formed pair-bonds with two males successively; one female nested with three males successively. In addition, one nest was destroyed and the female did not nest again; one female nested with two males, but her first male lost his brood and she nested with him a second time — her third clutch and his second; and finally, one nest hatched at which no female had been seen.

In 1971, five females initiated 12 nests; each female nested with the following numbers of males: two females remained monogamous; two females each had two mates; one female mated successively with four males. In addition, one nest hatched, and I had seen no female near it. Again, one male lost his first brood and his female nested with him again — her third clutch, his second.

Females shared the incubation of the final clutch with the male; but on previous nests, the males incubated and reared the young.

Of 34 young Spotted Sandpipers banded on Great Gull Island in 1967, 10 were seen later in the season, three up to eight weeks after hatching.

### *Acknowledgments*

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I wish to thank Dr. Theodora Nelson, who, having worked on Spotted Sandpipers at the University of Michigan Biological Station, suggested that I follow the females during the reproductive season to determine whether or not they mated with more than one male; Grace Donaldson, whose energy and enthusiasm enabled us to band 20 female Spotted Sandpipers in 1969 and to follow the banded young in 1967 and the adults in 1970 and 1971; Mary LeCroy, Lauren LeCroy, and Christopher Pineo for locating nests and broods in 1971; Charles Collins for notes on birds banded in 1967. In addition, I am most grateful to Desmond Nethersole-Thompson for promptly replying to my questions about the Dotterel; to Mary H. Clench for sending a reference; to Helmut Schiller for translations; to Isabelle S. Fries and Christopher Pineo for drawing the maps; and to Catherine Pessino, Mary LeCroy, Kenneth C. Parkes, and Dean Amadon for reading drafts of this paper and making helpful suggestions.

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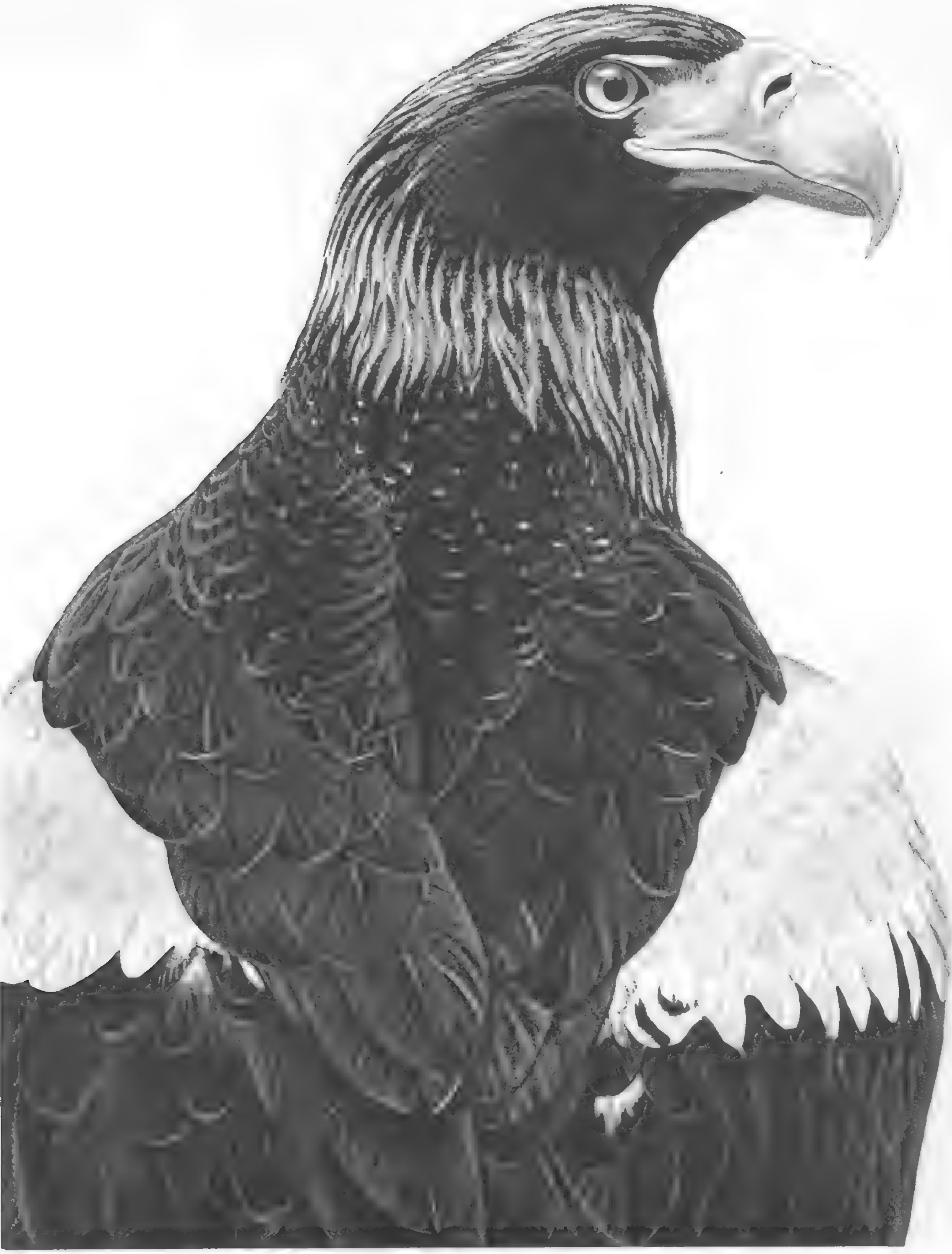

Sea Eagle, *Haliaeetus pelagicus*. Painting by Albert E. Gilbert.

# MONOGAMY AND POLYANDRY IN THE SPOTTED SANDPIPER

Lewis W. Oring and Merle L. Knudson
Photographs by the authors

In the preceding article, Hays (1972) convincingly demonstrated the existence of polyandry in an individually marked population of Spotted Sandpipers (*Actitis macularia*) on Great Gull Island, off the eastern tip of Long Island, New York. She found six of 11 females to be polyandrous in a population that averaged 1.9 males per female over a two-year period. The purpose of our paper is to compare Spotted Sandpiper polyandry in two Minnesota populations — one on the mainland in Itasca State Park and the other on a small island in Leech Lake, Cass County; to describe the nature of polyandrous mating systems in other shorebirds; and to theorize as to the evolution of polyandry in the Spotted Sandpiper.

The Spotted Sandpiper is one of a number of shorebird species for which polyandry has long been suspected. Female Spotted Sandpipers are larger, more heavily spotted, and more aggressive than males, which do most of the incubating and rearing of the brood. Similar sexual dimorphism and distribution of behavioral roles within the pair are found in the Common Sandpiper (*A. hypoleucos*), indicating that polyandry may be equally well developed in the Spotted Sandpiper's Old World counterpart (Oring, pers. observ.).

In the American Jacana (*Jacana spinosa*), Jenni and Collier (1972) demonstrated classical polyandry — females averaging 2.2 males per territory and the much smaller males setting up their own territories within areas defended by females. Hoffman (1949) described serial polyandry in the Pheasant-tailed Jacana (*Hydrophasianus chirurgus*) — females forming brief pair-bonds one at a time, with 7 to 10 males per season.

Nethersole-Thompson (1951; *in* Bannerman, 1961) reported that the Dotterel (*Eudromias morinellus*) was sometimes polyandrous, the larger females laying two clutches, each incubated by a different male. Walter Graul (pers. commun.) found that, in the Mountain Plover (*Eupoda montana*), pair-bonds were short-lived with males sometimes fertilizing second clutches for their original mates or for other females, and females sometimes laying second clutches with their first mate or a new mate. Both sexes incubated, but only one member of a pair incubated each nest.

In both Temminck's Stint (*Calidris temminckii*) and Sanderling (*C. alba*), females probably often lay two clutches — one incubated by each member of the pair (Hilden, 1965; Parmelee, 1970; Parmelee and Payne, in press). Parmelee (pers. commun.) believes that the Sanderling is sometimes serially polyandrous. A similar situation may occur in Temminck's Stint.

In the phalaropes (Phalaropodidae) and painted snipes (Rostratulidae), females are larger and more aggressive than males, and only males incubate and brood the young. These phenomena, along with disparate sex ratios, led to the idea that these groups exhibit polyandry (Beven, 1913; Nethersole-Thompson and T. E. Randall *in* Bannerman, 1961). Recently, Raner (1972) showed that in an individually marked population of four female and six male Northern Phalaropes (*Phalaropus lobatus*), two of the females laid two clutches for each of two males. In addition, Raner (1972) observed a possible incident of polyandry in the Spotted Redshank (*Tringa erythropus*). It appears that polyandry is a more common phenomenon than we previously supposed, its existence perhaps being masked by the fact that while the potential for polyandry may be genetically present, its expression may be dependent upon a particular set of environmental conditions which often are not present.

## Study Areas

The work reported here represents one aspect of a comprehensive study of Spotted Sandpiper behavior, conducted at Itasca State Park sewage lagoon, or LaSalle Lagoon, from 1969 to 1972. The lagoon, including the cleared area around it, is an isolated patch of Spotted Sandpiper habitat 6.8 hectares in size and surrounded by virgin forest for four or more kilometers in all directions (Figure 1). We have never known a breeding bird to leave the lagoon temporarily; other sandpipers rarely visit it except in migration. The cleared area around the lagoon is practically devoid of woody vegetation, and there are large areas where vegetative cover is scattered (Figure 2). On each of the more than 100 mornings spent at the lagoon, we recorded one or more potential predators, including red-sided garter snakes (*Thamnophis sirtalis*), six species of birds, and ten mammals.

Early in 1972, we began a study of Spotted Sandpiper behavior on Pelican Island in Leech Lake, a small island of 1.6 hectares within 0.5 km of three other islands, where Spotted Sandpipers do not breed, and 8 km from the mainland (Figures 3 and 4). The breeding sandpipers sometimes visited the other islands, but we never saw a bird flying to or from the mainland. The only evidence of predators observed in nine visits to the island were two garter snakes seen on each of two days, and feces, believed to be those of mink (*Mustela vison*), on one day. Ring-billed Gulls (*Larus delawarensis*) were always on or near the island, but we never saw them in areas where sandpipers bred.

## Methods

In 1969, four pairs of Spotted Sandpipers bred at the lagoon. We marked two males. In 1970, there were 11 breeding birds, five females and six males, and all but one female and one male were marked with colored plastic leg bands and enamel paint. In 1971, there were eight breeding birds, four females and four males, and seven were marked with colored plastic leg bands and Sanford's magic marker pens. In 1972, there were seven breeding birds, three females and four males, and all were marked with color bands and magic marker pens.

We caught birds by a variety of methods, the most efficient of which were funnel traps, placed along the shore in favorite feeding spots, and a 0.75-meter diameter spring-loaded nest trap. When properly used, the spring trap was 100 per cent effective.

In 1970, 1971, and 1972, we made observations from 05:00 to 10:00 and 18:30 to 20:30 hours every day from the time the birds arrived until hatching. During periods of peak activity, we watched almost continuously throughout the day. Additional observations, on a less regular basis, continued throughout the season until all birds fledged. From a number of high spots around the lagoon we could observe several pairs at once, and, with the help of various students

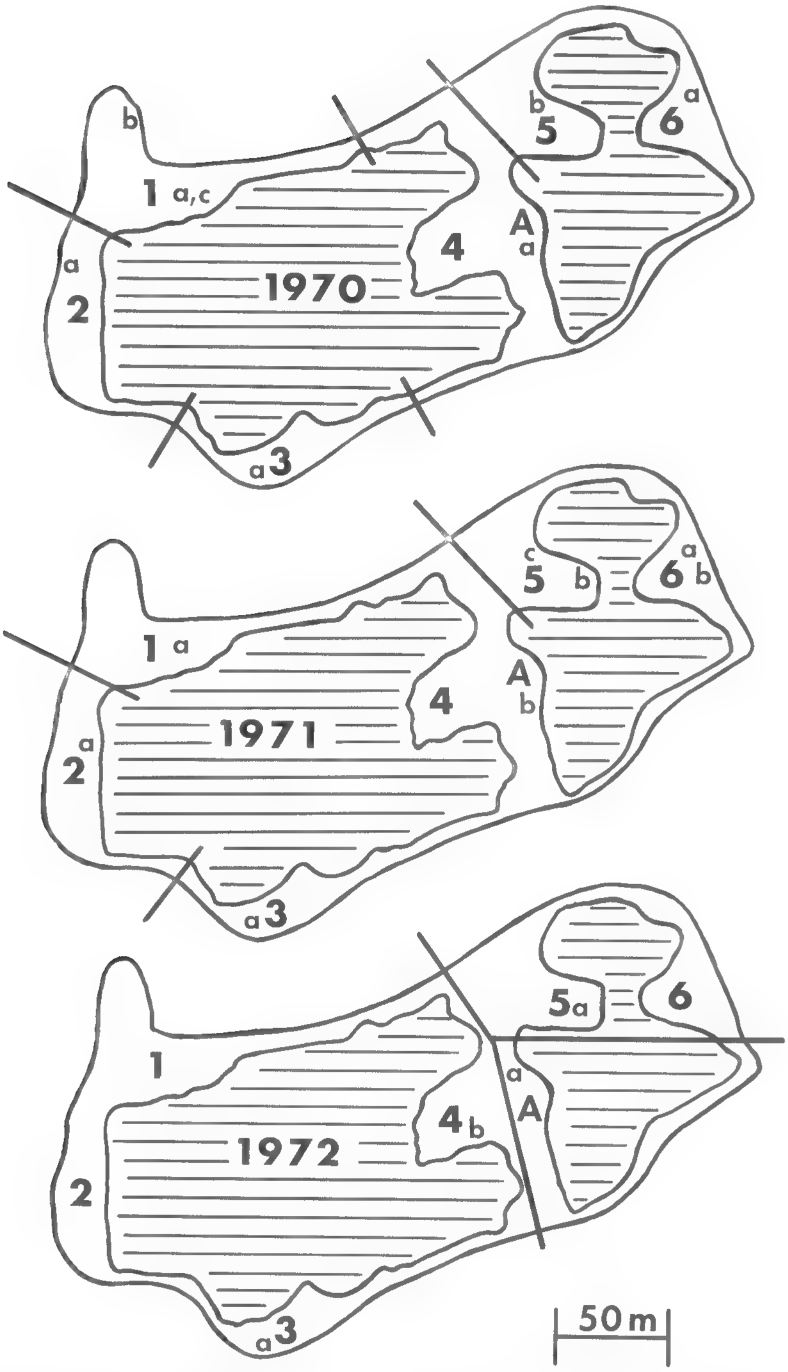

Figure 1. Lagoon maps showing territorial boundaries and nest locations for 1970–1972. Numbers one through six and large A indicate principal nesting areas; small letters indicate positions of nests in chronological order, a through c.

and staff at the University of Minnesota Biological Station, it was possible to monitor the nest-building, egg-laying, copulation, and incubation behavior of virtually every pair. We mapped territories by noting zones of conflict between adjacent pairs. Individual markers, as well as sexually dimorphic features, allowed us to identify accurately each individual and its sex.

We visited Pelican Island several times in 1969, 1970, and 1971, and on 24 May and 6, 13, 14, 21, and 27 June 1972. Two observers were present on 13 and 21 June, three on 14 June, and 13 on 27 June. Although we did not color band the birds, we were able to keep track of virtually every bird because three females had unmistakable plumage features and the island was very small. We ascertained the number of males as follows: on 21 June there were two newly hatched broods accompanied by males; seven nests where males were incubating; and one male prospecting for a nest site with his mate. On that same day, six females were simultaneously observed. We had collected a seventh female the week before. We estimated the total breeding population, therefore, as seven females and 10 males.

The vocalization terminology follows that of Knudson (1972). Epigamic vocalizations are those that tend to occur in reproductively motivated situations — e.g., in mate attraction.

## *Results*

In 1970, five females at Itasca State Park laid eight clutches while paired to six males. Four hatched and four were depredated (Table 1). Three females laid one clutch, one laid two, and one three. The females laid all replacement clutches in the same general area of the lagoon as their initial nests, but there was a tendency for these females to build their second nests at opposite ends of territories from original ones (Figure 1).

In 1971, four females laid seven clutches for four males. Two laid single clutches, one laid two, the other three. Three clutches hatched, two were destroyed, and two deserted (Table 1). No females were polyandrous. Female 74, which laid three clutches, alternated successive nests from one side of her original territory to the other. Female 5 laid her second clutch in a newly acquired territory more than 200 meters from her original nest and only 15 meters from where Female 74 had searched for a nest site at the start of the season.

In 1972, three females laid four clutches for four males. Two laid one clutch each; the third, Female 96, laid two, one for each of two males (Table 1). In order to form her second pair-bond, with Male 75, Female 96 moved over 200 meters to an area so close to the territory of Female 72 that fighting occupied most of three days. The two nests were 43 meters apart. Of four clutches laid, one was completed 21 May and another 23 May. The female, which laid the clutch on 21 May, completed another for her second mate on 29 May. The fourth clutch, completed on 5 June, was laid by a female which did not arrive until 29 May and which probably bred elsewhere before coming to the lagoon.

None of the 1972 clutches hatched; three were depredated and one was deserted in a severe thunderstorm. Immediately following each catastrophe, the birds involved disappeared. After 26 June, no sandpipers were present at the lagoon, whereas in years when four or five females bred, renesting persisted into early June.

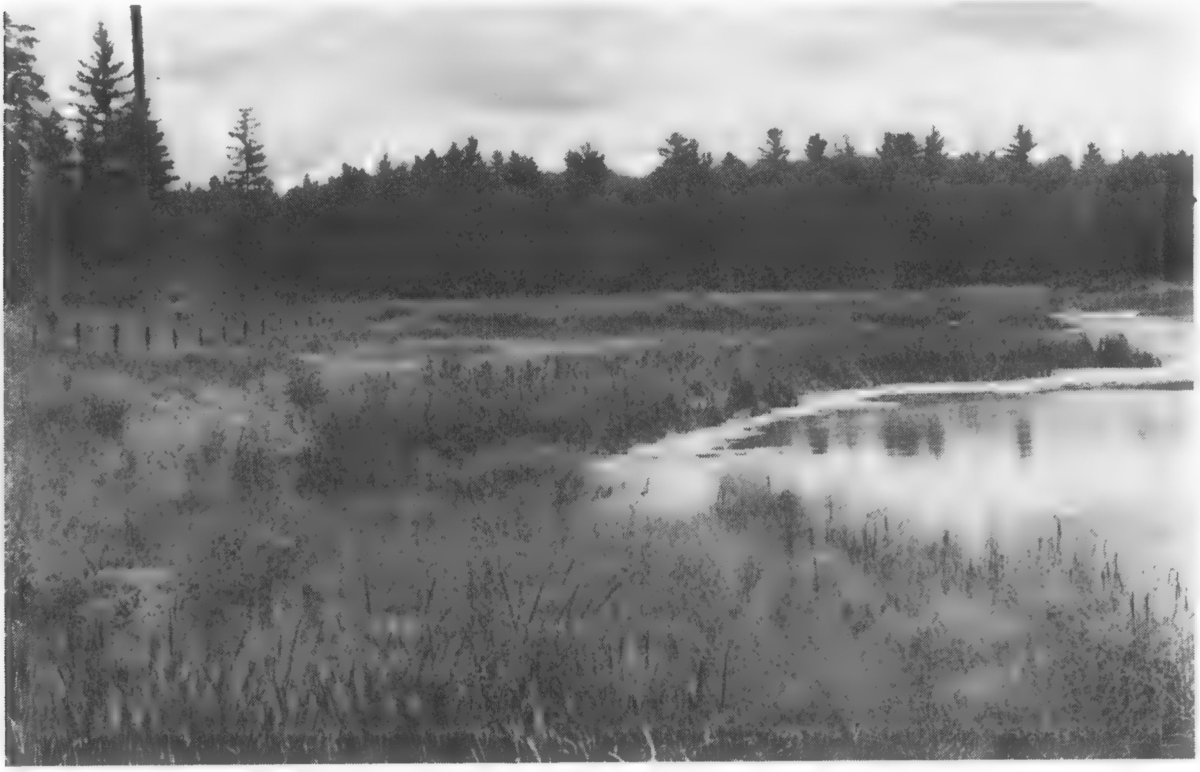

Figure 2. Breeding Area 1 at the lagoon at the time of hatching. When nest sites were being chosen, this sandy area had scattered herbaceous and grassy cover less than 10 centimeters high.

TABLE 1

Mating Histories of Spotted Sandpipers at Lake Itasca, Minnesota, 1970–1972

| *Female number* | *Year* | *Male* | *Area number* | *Clutches hatched* | *Clutches depredated* | *Clutches deserted* |
|---|---|---|---|---|---|---|
| 72 | 1970 | 70 | 1, 1, 1 | 1 | 2 | – |
| 72 | 1971 | 70 | 1 | 1 | – | – |
| 72 | 1972 | 20 | 4a | – | – | 1 |
| 73 | 1970 | 75 | 3 | 1 | – | – |
| 74 | 1970 | 78 | 6 | – | 1 | – |
| 74 | 1970 | UnM* | 5 | – | 1 | – |
| 74 | 1971 | UnM* | 6, 5–6**, 5 | – | 1.5 | 1.5 |
| YG† | 1970 | 71 | 2 | 1 | – | – |
| UnM* | 1970 | B1† | 4a | 1 | – | – |
| 96 | 1971 | 71 | 2 | 1 | – | – |
| 96 | 1972 | 71 | 3 | – | 1 | – |
| 96 | 1972 | 75 | 5 | – | 1 | – |
| 5 | 1971 | 75 | 3, 4a | 1 | – | 1 |
| 19 | 1972 | 21 | 5 | – | 1 | – |

*Unmarked.

**First two eggs destroyed in Area 5, the second two laid, then deserted, in Area 6. Tabulated in totals as a depredated clutch.

†Color marked only.

In 1970, two surplus males visited the lagoon — one, which was expelled during the initiation of pair-bonds, and another, which arrived just as Female 74 was completing her first clutch. This latter male became Female 74's second mate. In 1971, we banded four surplus males early in the season and there may have been additional ones, but none remained to form pair-bonds with resident females. In 1972, one or two extra males visited the lagoon briefly at the start of the season, but the residents chased them off. Another surplus male arrived late in the season — the morning of the day when one female was to lay her third egg and another female her first. This late arrival paired with the female which laid her fourth egg the day he arrived, and she moved more than 200 meters to join him. The following account of this incident of polyandry illustrates the intensity of aggression directed toward surplus males, as well as the site tenacity which some males exhibit.

On 20 May, Female 72 laid her first egg early in the morning on the dike separating Areas 4 and 5, and Female 96 laid her third egg late in the morning in Area 2. The total number of songs between 05:30 and 08:30 on the previous two days had been 45 and 33, respectively, with the females doing most of the vocalizing. At daybreak, a male had arrived, which had incubated two clutches in 1971, one in Area 3 and the other between Areas 4 and 5. When he came directly to the dike where he had incubated last in 1971, there was a great amount of vocalizing — 67 songs and 27 epigamic calls from 05:30 to 08:30 — with most of the singing by the males. On the previous morning, the resident male had been relatively silent. Chasing followed, and, as is usually the case during egg-laying, the resident male did most of the chasing. The newcomer, Male 75, persistently returned to the area following chases.

The next day, song rates remained high — 69 songs and 10 epigamic calls in three hours — and so many chases took place, the majority of which erupted into prolonged aerial chases high above the lagoon, that a count was impossible. The birds spent 27 minutes of one 30-minute period chasing, mostly in the air. However, by 10:00 the chasing had subsided and Male 75 was appeasing Male 20 on the dike and chasing him from Area 4. Late that afternoon, Female 96 laid her fourth egg for Male 71 and immediately took up residence with Male 75. She fought intensely with Female 72 that evening along the dike.

Female 96 spent 22 May in Area 4 with her new mate. Much of the time she spent fighting with Female 72 which laid her third egg that day. Both females were again sexually active and they dominated the aggression between the two pairs. Between 05:30 and 08:30 there were 98 songs and 42 epigamic calls — a large increase over previous days in both aggressive and reproductively motivated vocalizations.

The next day, 23 May, fighting was brief and sporadic, and vocalizations dropped to 85 songs and 17 epigamic calls from 05:30–08:30. Nest site prospecting and nest-building occupied most of the new pair's time. The female laid her first egg early on 26 May in Area 4. By that time, vocalizations had decreased to six songs and no epigamic calls from 05:30–08:30.

Seven of the 10 breeding males, marked during the course of this study, returned the next year to breed at the lagoon; and one of the three, which did not return to breed, nested at a small pond 4 km away. Four of seven females returned in subsequent years, and an additional banded female, without a color band, bred 4 km north of the lagoon. This female may have been a lagoon-breeding bird, which lost her color band, or a young female hatched at the lagoon. However, of 16 chicks banded at the lagoon in 1970 and 11 banded in 1971, none have yet returned.

Of the seven marked males that bred at the lagoon in successive years, only one had his first nest in the second year outside the territory where his last nest of the preceding year had been. One male moved approximately 150 meters to breed in an adjacent but unoccupied territory. Another, which left the lagoon in 1970 after his nest was destroyed and while his mate was paired with a new male, bred 4 km north of the lagoon in 1971.

Of the four marked females that returned to breed, two nested with the same males and in the same territories as their last nests of the previous year and two bred in areas more than 150 meters away. One of the two females that moved was paired to a new male; the other arrived with her previous mate and they moved together 100 meters to a new territory.

In three cases, both members of a marked breeding pair returned to breed at the lagoon, and their first pair-bonds were with their former mates. In one case, Female 72 in 1971, was already paired to, and copulating with, a new male when her former mate arrived. She tolerated her former mate which then drove off the new male. This female laid her first egg the second day after her old mate arrived — in the very scrape in which the pair hatched a clutch the previous year. We have never known a female to lay an egg in less than three days from the time her pair-bond was formed or her nest lost, indicating that in this case one male was responsible for the female's initial ovarian development, and another male for fertilizing her eggs.

### Pair-bond Formation

Little time is required for the formation of a pair-bond. When the males first arrived in spring, there was usually a surplus of females, and aggression around the males was so intense and chases so frequent and prolonged, that it was difficult to determine when a bond was or was not formed. However, it appears that even the first pair-bonds of the season are formed within a few minutes of the male's arrival—when he leaves the shoreline and enters nesting cover with a female. From that point on, we have observed no changes in pair relationships until after laying, except when one member of a pair was killed or caught in a trap. We observed pair-bonding of late arriving males more easily because they returned to the spots where they had incubated the previous year or, in the case of new males, to areas of high activity. Several minutes after encountering an unpaired female, the male and female formed a pair-bond though, in some cases, a day passed before they were able to approach each other closely enough to allow copulation. The following resumé of the arrival of Male 20 illustrates the rapidity of pair-formation.

Two unmarked males arrived at the lagoon at daybreak on 15 May 1972. About 10:10, after unsuccessfully attempting to settle in an area already holding an established pair, they entered the territory of an unpaired female, Female 72, which had arrived five days earlier and established herself in Areas 4 and 5, some 200 meters from where she had bred in 1970 and 1971. Within 15 minutes of their arrival in the territory of Female 72, there were two male-male fights, three chases, 31 songs, 18 epigamic vocalizations, and six slow songs.

One hour and seven minutes after they entered Female 72's territory, one male had established his superiority over the other and was running into nesting cover with tail down, followed by the female in tail-up posture and the second male. The female intermittently turned and chased the second male. After a few initial runs into nesting cover, the pair flew to the shore and fed. Throughout the day both male and female sang frequently, averaging about one song per minute. At one point, the male flew to the female in an apparent copulation attempt, but the female threatened him and then immediately assumed the reproductively motivated tail-up posture. At 16:08, the female walked into the nesting cover, the male followed, and nest site prospecting began. The next morning the pair began copulating; the female laid the first egg on 20 May, just five days after the arrival of the male.

### Incubation

Following the laying of the third egg, there is an increase in female sexual and aggressive activity, which is manifested by higher singing rates and either an increase in territorial defense or in the number of intrusions into other territories where sexual or aggressive activity is going on, or both. There is, however, a good deal of individual variation in the nature of female behavior after laying, perhaps mediated by the amount of activity nearby. Some females begin incubating with, or before, the laying of the fourth egg, whereas others show a sudden surge in sexual activity and only begin incubating after several

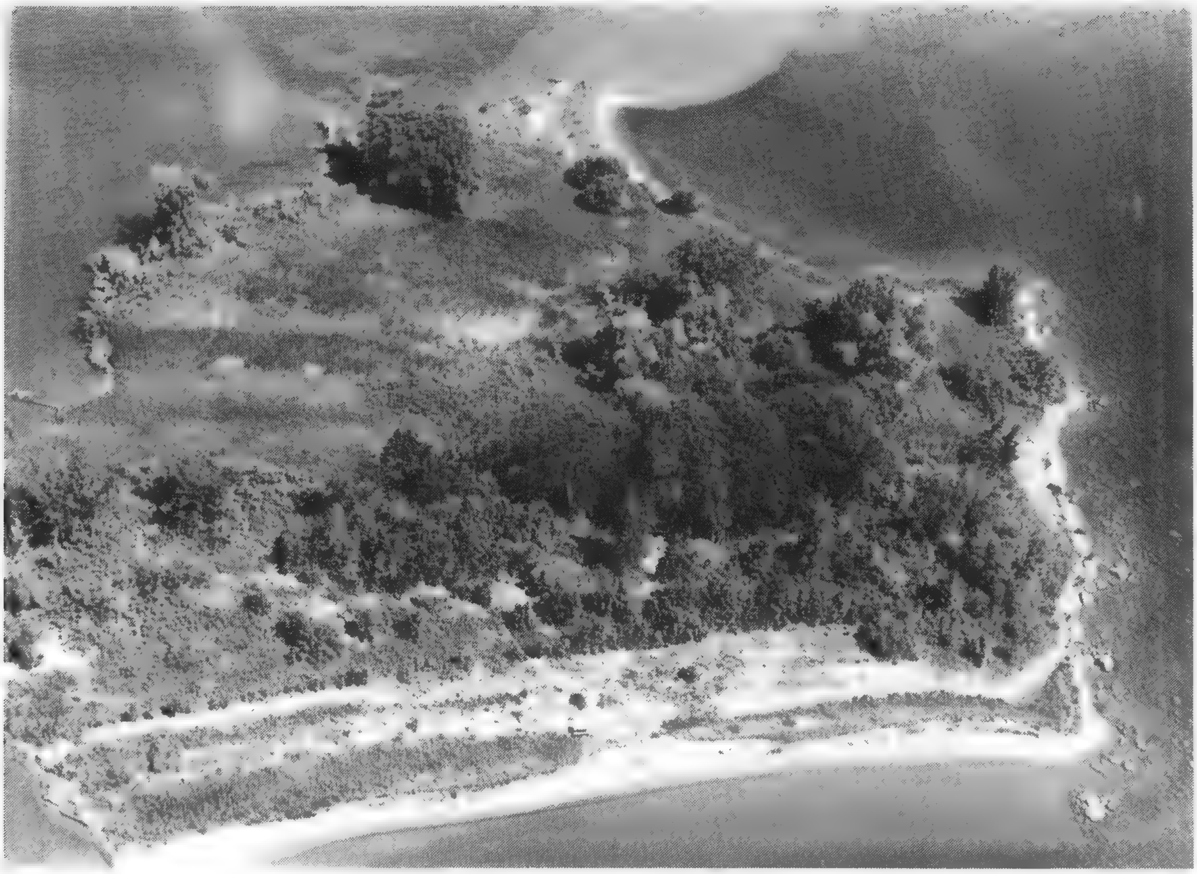

Figure 3. Aerial photograph of Pelican Island. Seven of nine original nests were on that part of the island shown in the lower left, one-fourth of the picture. Four of these nests were on or near the main beach and three were beneath dense shrubs and trees. The other two nests were at the tips of the island at the extreme top and lower right of the photograph.

days of extensive singing and aerial advertisement. Presumably, females which show the greatest increase in post-laying sexual activity and the weakest incubation tendencies are those most likely to form bonds with second males, should surplus males be available.

In 1972, Female 19 proved to be the most frequently incubating female we studied. She began incubating a few hours before she laid the fourth egg, and, near the end of the incubation period, she sat from early morning until late afternoon. Still, her singing rate, which had decreased sharply during the early part of the egg-laying period, increased greatly after she laid the third egg (Figure 5). She sang over other territories too and, on several occasions, was expelled from them. She did not, however, move to any unoccupied areas to establish a new territory although one-half of the lagoon was vacant.

Female 5, in 1971, did not incubate during the first four days of incubation. Not only did her singing rate increase after laying the third egg, but she began visiting all areas of sandpiper activity, displaying sexually to males, attempting to expel females, and centering her activity largely around a male whose mate had left the lagoon and which was being coveted at the time by a newly arrived female. Female 5 attempted for three days to form a pair-bond with this male and, after being expelled 10 times in four days by two other females in the vicinity, established a territory in an unoccupied area at the other end of the lagoon. She spent an entire day singing over and around this new area prior to the time we trapped her original mate which promptly deserted his nest and rejoined her. They renested, this time in a new area which she had claimed, 200 meters from the first nest. This male was the only one to desert following nest-trapping.

During the time of post-laying sexual resurgence, females incubated briefly, usually sometime between 06:30–09:00 and 19:30–21:00, or both periods. There was a good deal of individual variation in the amount of time females spent incubating independent of weather and stage of cycle, but all of the eight females, whose incubation patterns we studied, showed a general tendency to incubate more in the later part of the incubation period and in cold, rainy, or windy weather. Females that had been sitting on the nest regularly sometimes skipped incubation completely on warm days.

### Replacement Clutches

The initiation of replacement clutches or clutches for second mates averaged 5.3 days after predation or desertion. In two cases, in which the female was sexually active but not yet incubating, the first eggs of the new clutches were laid 3.5 and 5 days after loss of the nest or desertion of mate. In three nests with incubating females, the first eggs of the replacement clutches were laid four, four, and six days after predation. Another female waited 10 days after deserting an unincubated, but partially destroyed, second clutch before laying the first egg of her third clutch.

### Instability of Pair-bonds

Pair-bonds break as rapidly as they form. As mentioned above, Female 72 had formed a pair-bond and was copulating with a new male in 1971 when her mate of 1969 and 1970 arrived. It was only a matter of minutes before she paired with her former mate. We observed another equally rapid pair-bond switch earlier in 1971, involving this same female. Female 96 had been paired to, and copulating with, Male 71 for eight days. Their nest was already lined on the morning of 22 May when we caught Female 96 in a trap. Less than

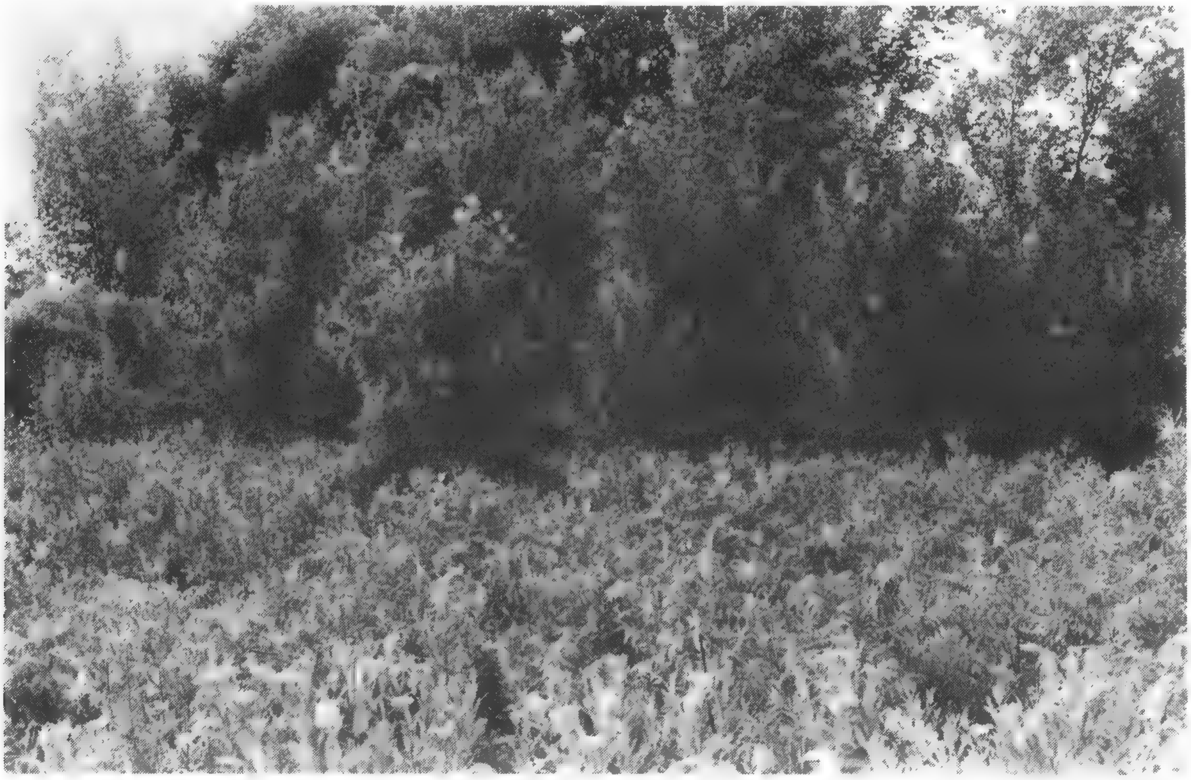

Figure 4. Area of Pelican Island where seven nests were located, showing herbaceous vegetation which harbored four nests (foreground) and woody vegetation which surrounded three (background). All vegetation was growing on sand. Herbaceous plant cover was approximately 0.5 meter high and extended 30 meters from the beach toward the island's center. The mixed deciduous woods was 20 to 50 meters from the beach and had a canopy 8 to 13 meters high.

15 minutes later we saw Male 71 copulating with Female 72 which had been unpaired previously. In addition, he defended her territory against an intruding male and followed his new mate into nesting cover. We released Female 96 from the trap 15 minutes after Male 71 and Female 72 had copulated. She flew directly to her nest. Observations of the birds concerned were discontinuous after this time. However, Female 96 and Male 71 were again nest-building together the following morning, and their first egg was laid early 25 May. Female 72 thus copulated with three different males between 22 and 24 May when her old mate finally arrived.

## Pelican Island Population

The 1972 breeding population included an estimated 1.43 males per female. The seven females laid a minimum of 13 clutches including two replacement clutches — after we had removed the first clutch — and one following the single incident of predation. Back-dating 21 days from the date of first hatching on the island, the three earliest clutches were completed on 28 or 29 May. Single eggs were taken from all nests being incubated on 27 June. They hatched in an incubator at various times up to 18 July. On 27 June, a pair, whose eggs were removed, immediately began prospecting for another nest site. If they had laid a new clutch, the eggs would not have hatched until the end of July.

In 1972, we kept track of eight clutches for a total of 127 clutch days; in 1971, we observed a single nest for over 14 additional days. Only one nest was depredated during this time — a garter snake destroyed it while we were on the island on 21 June 1972. Assuming a 21-day incubation period, 141 clutch days are equal to approximately 6.7 incubation periods; and one case of predation in 6.7 incubation periods provides an estimated predation rate of 15 per cent.

Nine original clutches on Pelican Island in 1972 averaged 3.4 eggs. Five of the nine nests were on the island's main beach, the site of daily visits by fishermen between 11:30 and 13:30. As a result of the almost certain disturbance, four of five beach nests had reduced clutch sizes — 3, 3, 3, 2 — while a fifth on the beach and four nests elsewhere on the island had normal clutches of four eggs.

## Comparison of LaSalle Lagoon and Pelican Island

The breeding density of Pelican Island in 1972 was 7 to 10 times that at the lagoon in various years despite the fact that nest sites and food appeared to be more readily available at the lagoon. In addition, the number of available males was greater on the island than at the lagoon — 1.43 versus 1.17 males per female. Disparities in breeding density and the ratios of males to females are attributed to the differences in predation rates — 47 per cent at the lagoon and 15 per cent on the island. Since males are far more susceptible to predation because of their predominant role in incubation, the greater number of males on the island is easy to account for. Differences in predation rates between the two study areas may have been even higher in past years. This was the first year that we noted garter snakes on the island.

Sandpipers used all the sparsely vegetated areas on the island as nest sites. Seven nests, simultaneously active on one quarter of the island, were so close together that the greatest distance separating any two nests — 37 meters — was less than the distance between the closest two nests at the lagoon — 43 meters. We found no nests in the densely wooded area surrounding the lagoon,

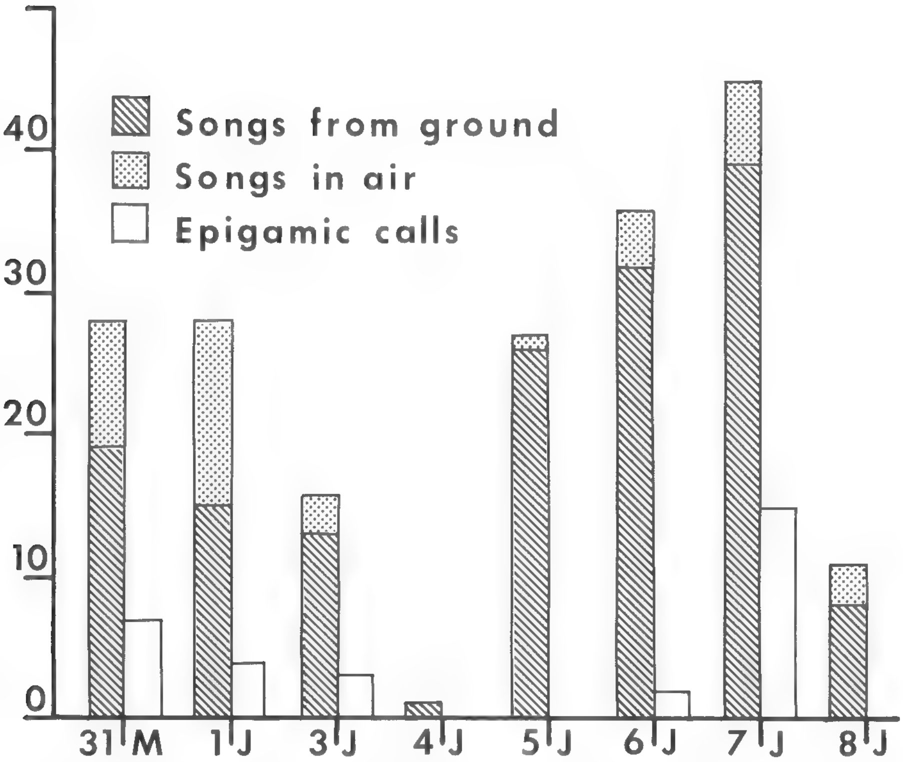

Figure 5. Total number of songs and epigamic calls at the lagoon from 05:30–08:30, 31 May to 8 June 1972. Female 19 laid her first egg 05:40, 2 June; her third 10:00, 4 June. Six birds, three males and three females, were present. Virtually all vocalizations were uttered by Female 19 and an adjacent female.

whereas on the island we found three of the nine original nests, in 1972, beneath dense shrubs or trees. Aggressive behavior was much more frequent and intense on the island than at the lagoon. Furthermore, it continued much longer each day and extended farther into the season. Aggressive responses to song playbacks were three times greater on the island than at the lagoon (Knudson, 1972).

Because of the high degree of overt aggression on the island, the sandpipers began their nests about a week later than at the lagoon. Also, with a few exceptions, sandpipers never firmly established territorial boundaries on the island, and intense aggression continued throughout the season. However, at the lagoon, birds always established firm boundaries within a couple of days of arrival, after which overt aggression was rare unless new birds arrived. Disturbances by fishermen not only brought about reduced clutch sizes on the island, but probably, in conjunction with intense aggression, caused the birds to nest in marginal habitats.

## *Discussion*

Those individuals making the greatest contribution to the gene pool of future generations are, biologically speaking, the most successful. However, as the number of offspring increases, counter selective forces, such as limited food supply for young, decreased parental care, and increased stress on the female, come into play. In shorebird species where predation rates are high and food supplies great and seasonally prolonged, one would expect that there might be selection for multiple clutches — either in conjunction with monogamy or polyandry. Various environmental factors bringing about instability— for example, relatively frequent storms for shoreline breeding species, or unpredictable food supplies due to drought for species in arid environments —

might act in much the same manner as a high rate of predation. Where multiple clutches have evolved, it is likely that it has come about with certain compromises which minimize female stress, such as advanced age at first breeding, assumption by the male of certain stressful behaviors such as incubation and brood rearing, or a reduction in the size of the clutch or egg.

The Spotted Sandpiper is one of a few scolopacids that successfully colonized the south temperate parts of North America. In doing so, it occupied areas with longer periods of high food supply and longer summers in which to rear young, thus increasing the potential for multiple clutches. At the same time, the southern colonization brought the species into contact with a number of new ground predators, including snakes, and a whole host of southern mammals.

The fact that Spotted Sandpipers breeding on the mainland are subjected to high predation is indicated by the 47 per cent rate of egg predation at the lagoon. The sparsely vegetated areas where Spotted Sandpipers nest are not only frequented by mammals hunting around the water's edge, but also by snakes seeking sunning spots or hunting frogs. The highly ritualized distraction display and unique squealing vocalization associated with it indicate that a high rate of predation has long been a part of the pressures facing Spotted Sandpipers.

Spotted Sandpipers in Minnesota certainly are capable of laying multiple clutches because food supplies remain high throughout most of the summer, pair-bonds are rapidly formed and broken, and the period between clutches is brief. Two females at the lagoon each laid three clutches in a single year (Table 1). Young from only one of these clutches hatched, and they fledged successfully. Likewise, we know that one parent alone can successfully incubate because, of four clutches incubated solely by the male, three hatched; the fourth was destroyed by a predator.

The Spotted Sandpiper thus has evolved the potential for serial polyandry in conjunction with increased length of the breeding season and high predation rates encountered during its southern colonization. In the face of the instability caused by predation, natural selection probably favored a mating system that increased the total number of offspring, in spite of the concomitant increase in stress to the female. At the same time, natural selection favored the evolution of greater participation by the male in incubation and brood-rearing, a slight increase in the female to egg-weight ratio, and possibly a delay in the age at which females first breed. Orians (1969) pointed out that unless females are able to recover sufficiently between successive clutches, there is no advantage in increasing the production of offspring.

On islands, where instability due to predation is minimal, serial polyandry is more common than on the mainland where the predation pressures that gave rise to the system are manifested. What seems to be a paradox is due to the large number of surplus males available in the absence of predation; for during the course of the species' evolution, females developed behavioral and physiological mechanisms that allowed them to breed repeatedly whenever surplus males were available.

Similar characteristics, indicative of compromises selected for during the evolution of Spotted Sandpiper polyandry, are exhibited to a greater or lesser extent by phalaropes, painted snipes, jacanas, Dotterels, and Common Sandpipers (Table 2). Among the shorebird species for which polyandry has been suggested and multiple clutching demonstrated, only the Mountain Plover and Sanderling deviate with regard to these characters. In the case of the Mountain Plover, Graul (pers. commun.) showed that the mating system is complex and variable, and he attributes its evolution largely to the lack of stability in their short-grass prairie environment. Considering the extreme conditions under which Sanderlings nest in the high arctic, there is little doubt but that whatever their system eventually proves to be, it will show adaptations for highly unpredictable food supplies, short seasons, and rigorous climatic conditions in contrast to polyandrous systems which have evolved in areas with high predation rates, long seasons, and abundant food.

It appears that various types of polygamous mating systems, including polyandrous ones, are more common among shorebirds than we previously supposed. Within the suborder Charadrii, certain species occupy some of the harshest arctic and arid environments, others the temperate forests and grasslands, and still others various tropical habitats. These species are exposed to the diversity of food supplies, season lengths, and predation pressures typical of their environments. In response to this great array of selective pressures, a large variety of social systems has evolved. Where a system of multiple clutches of various types has evolved, we find various compromises reducing female stress. Studies of those species exhibiting these compromise characteristics will undoubtedly reveal new and interesting cases of polyandry.

TABLE 2

Characteristics of Some Shorebirds for Which Polyandry Has Been Demonstrated or Suggested*

| | *Female 3 per cent larger than male* | *Egg or clutch size reduced* | *Female dominant in courtship* | *Male does most incubating* |
|---|---|---|---|---|
| American Jacana<br>(*Jacana spinosa*) | ++ | ++ | + | ++ |
| Pheasant-tailed Jacana<br>(*Hydrophasianus chirurgus*) | ++ | ++ | + | ++ |
| Spotted Sandpiper<br>(*Actitis macularia*) | + | + | + | + |
| Common Sandpiper<br>(*A. hypoleucos*) | + | + | + | + |
| phalaropes<br>(three species) | ++ | ++ | + | ++ |
| painted snipes<br>(two species) | ++ | + | + | ++ |
| Dotterel<br>(*Eudromias morinellus*) | + | + | + | ++ |
| Mountain Plover<br>(*Eupoda montana*) | — | + | — | — |
| Sanderling<br>(*Calidris alba*) | — | + | — | — |

*Compiled from Dement'ev *et al.*, 1969; Mackworth-Praed and Grant, 1962; Parmelee, pers. commun.; Ridgway, 1919; Witherby *et al.*, 1940; and personal observations. Plus marks indicate relative expression of the various characteristics; dashes indicate the lack of the characters mentioned.

## Summary

We studied the mating patterns of an individually marked population of Spotted Sandpipers (*Actitis macularia*) from 1970 to 1972 at a 6.8-hectare sewage lagoon in Itasca State Park, Minnesota, and an unmarked population in 1972 on a 1.6-hectare island in Leech Lake, Minnesota.

At Itasca, 12 females laid 19 clutches for 14 males. Only two females bred with a second male in a single year, yielding an average of 1.17 males per female. Seven clutches, 37 per cent, hatched; nine, 47 per cent, were destroyed by predators; and three, 16 per cent, were deserted. Surplus males were rare and were chased intensely by resident males.

Seven of 10 marked breeding males and four of seven marked females returned to breed the following year. Six of seven returning males and two of four returning females bred in the same territories where they last bred the preceding year. In three cases, both members of a pair returned and each time the old pairs were formed again.

Pair-bonds were formed in a matter of minutes, but once birds paired, there was no evidence of promiscuity. Following the laying of the third egg, we saw a marked sexual resurgence in females, whether they commenced incubation or not. Female incubation was highly variable depending on the stage of cycle, the individual concerned, and the weather. Replacement clutches were initiated an average of 5.3 days after predation or desertion.

Seven females bred with 10 males on Pelican Island in 1972, yielding an average of 1.43 males per female. The rate of predation was approximately 15 per cent, and clutch size was reduced by disturbance from fishermen during egg-laying. The high breeding density on the island led to late nesting, intense aggression, territorial instability, and the use of marginal nesting habitat.

The fact that Spotted Sandpipers have had a long association with heavy predation is indicated by their highly ritualized distraction display. Their colonization of temperate areas, however, increased the length of their breeding season. These factors, and food availability over a longer season, have led to the evolution of serial polyandry. During the evolution of serial polyandry, counter selection brought about certain compromises in the form of a slight increase in the ratio of the weight of the female to the weight of the egg, increased role of males in such stressful behaviors as incubation and brood-rearing, and possibly a delayed age at which females first breed.

### *Acknowledgments*

We are indebted to Walter Graul for allowing us access to unpublished information gathered in his fine study of Mountain Plovers. Conversations with Donald Jenni, Gordon Orians, and David Parmelee were of immense benefit during the evolution of this study. Robert Seabloom critically read the manuscript.

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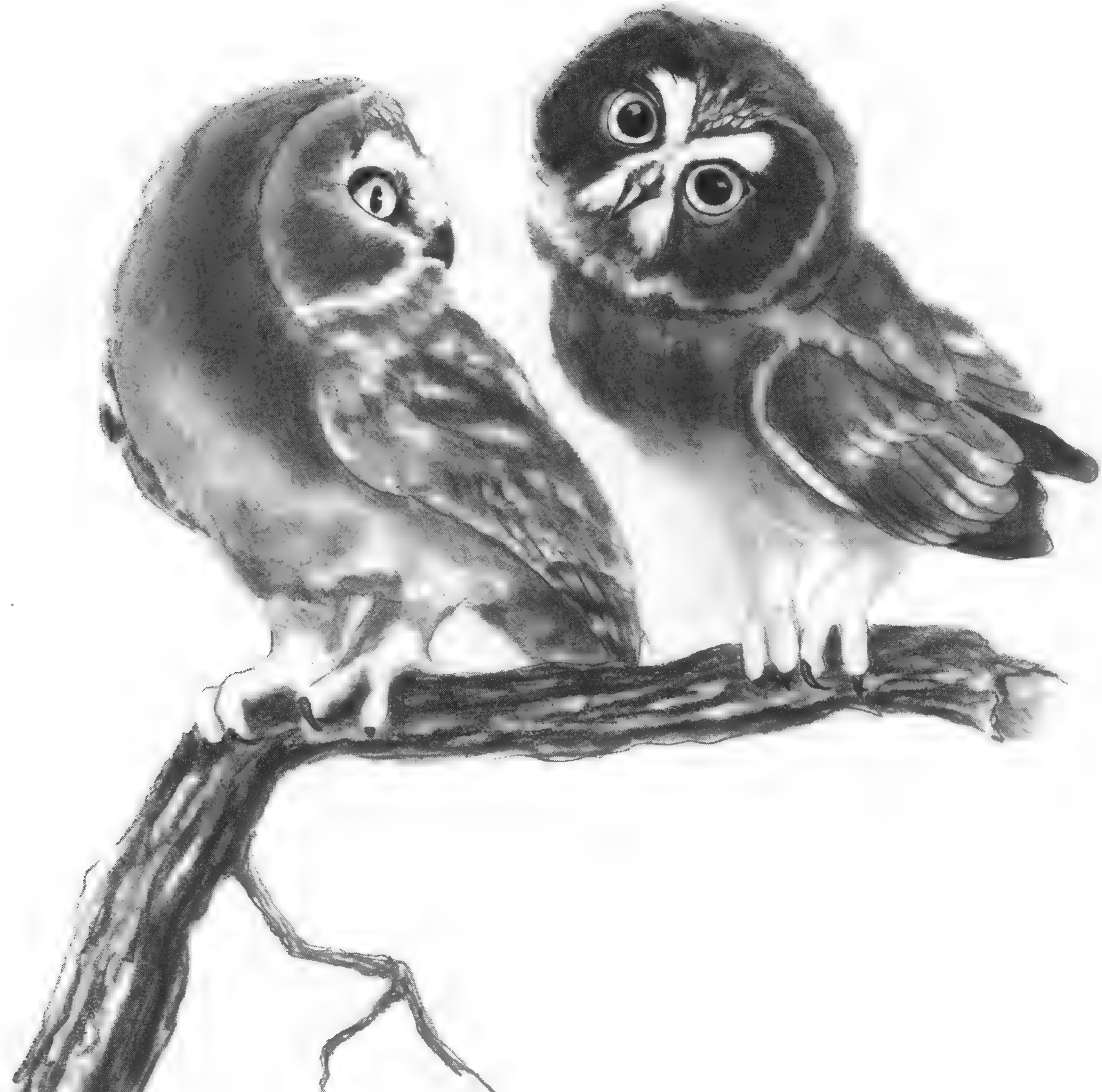

Saw-whet Owls, *Aegolius acadicus*. Drawing by Tony Angell.

# THE BIOLOGY OF AFRICAN BEE-EATERS

C. Hilary Fry

Photographs by the author

Found throughout the hotter parts of the Old World, the bee-eaters comprise a small and uniform family (Meropidae) of bright-plumaged and attractive coraciiform birds. In the hey-day of sumptuous bird monographs they received admirable treatment by Dresser (1884–1886), but since then they have all been neglected except for the single temperate-zone species, the European Bee-eater (*Merops apiaster*) that was well studied 10 years ago.

Ornithologists and laymen alike find bee-eaters most appealing because of the combination of handsome plumage and pleasing proportions, melodious voices, gregariousness, and confiding dispositions. There are many additional attractions, such as their use of living animals as perches and their breeding colonies so spectacular as to be featured in national tourist brochures. The birds are aptly named, for honeybees (*Apis mellifera*) and other Hymenoptera, often venomous, form a large part of their insect diet. Few other birds have evolved the capacity to exploit regularly this abundant food resource.

Seventeen of the 24 species of bee-eaters occur in Africa, where I have seen all but one and have studied several savanna species in some detail. The outstanding bee-eater, the Black-headed (*Merops* [*Bombylonax*] *breweri*) of the Congo forests, is in fact the only African one which may prove to be generically distinct (Fry, 1969b). All the others, whether forest or savanna birds in Africa, are remarkably uniform ecologically and morphologically, although there is considerable diversity in plumage (Bannerman, 1953; Fry, 1967a).

## *Habitats and Evolution*

Inhabiting the forests of southeast Asia, from the foothills of the western Himalayas to Hainan and Java, are two large bee-eaters which have a generalized arthropod diet. They are the Blue-bearded Bee-eater (*Nyctyornis athertoni*) and the Red-bearded Bee-eater (*N. amicta*), and in many respects they resemble the rollers *Coracias* (Coraciidae) rather than typical bee-eaters. Their plumage is a gaudy combination of yellow and grass-green with blue or scarlet and pink; voices are a harsh roller-like cawing; wings are rounded, bills heavy and arched; and — like rollers — they hawk for insects, including bees, on the wing, but feed mainly by pouncing on beetles, woodlice, millipedes, and small lizards on the ground (references in Fry, 1969b).

These characters are mostly in sharp contrast with *Merops* bee-eaters, particularly in respect to their specialized bee diet. *Nyctyornis* is more likely to be primitive than despecialized, indicating that the Asian forest was the likely place of origin of the family. Early bee-eaters are thought to have ranged through the Old World forests into Africa and to have made the difficult evolutionary transition from the forest to the savanna habitat only on that continent (Fry, 1969b). Speciation in the African savannas probably followed rapidly, and a few species of *Merops* managed to return to Asia via unforested biomes.

Today, two of the 17 African bee-eaters occur also in Asia. The Little Green Bee-eater (*M. orientalis*) does not migrate and its range extends across northern tropical Africa from Senegal to Eritrea, through the Arabian Peninsula to India and China. The migratory Large Green Bee-eater (*M. superciliosus*) has one race that breeds around the edge of the Sahara, another in Madagascar and sporadically in eastern Africa, and a third in the Middle East, replaced from India through Southeast Asia to New Guinea by the closely related Blue-tailed Bee-eater (*M. philippinus*). These birds, together with the Australian Rainbow-bird (*M. ornatus*) and two other Asiatic species of *Merops*, all inhabit open country and, from what little we know of their biology, seem to resemble closely the European Bee-eater and the bee-eaters of the African savanna in their salient features.

Besides *Nyctyornis*, four bee-eaters inhabit forests. Two, the Celebes Bee-eater (*Meropogon forsteni*) and the Black-headed Bee-eater, are vary rare in museum collections and have hardly even been seen by ornithologists. The other two inhabit the equatorial forests of Africa and, though our information is sparse, it is certain that their diets, feeding behavior, and breeding biology are much like those of the better known savanna bee-eaters.

Strictly speaking, the African nonforest, or savanna, species should number 13, not 14, but I have included the European Bee-eater because it winters throughout the savannas south of the Sahara and for some decades has been nesting sporadically in southern Africa. Most of them have green plumage, often with buff underparts, and always with contrastingly colored throats and black masks. In some bee-eaters the greens are suffused or masked with copper and in others with blue. Two savanna species have scarlet throats as do the forest Black Bee-eater (*M. gularis*) and Blue-headed Bee-eater (*M. muelleri;* Plate I); another has pink and slate-gray plumage, while the Carmine Bee-eater (*M. nubicus*) is carmine, pink, and blue (Figure 18). In addition, the 24 species differ in size — weighing from 15 to 60 grams — and in voice, wing shape, and tail shape. In view of this diversity, the ecological uniformity of the savanna bee-eaters of Africa is all the more remarkable. They differ in habitat, breeding season, gregariousness, mobility, nest conformation, and diet (Figure 1) — but these differences are much smaller among bee-eaters than among species of the same genus that inhabit the same area in the temperate zone — for example, gulls of the genus *Larus*, thrushes of the genus *Turdus*, or crows of the genus *Corvus* — and often the ecological significance of the differences we see is obscure.

## *Breeding Biology*

All bee-eaters nest in the ground in tunnels, which they generally excavate themselves anew each year, although they sometimes use last year's tunnels. Rarely, they may use old rodent holes (Mackworth-Praed and Grant, 1970), but the drive to excavate is so strong that the birds always modify preexisting tunnels to satisfy it. Tunnels vary in length from about one-half to one meter in the Least Bee-eater (*M. pusillus*, Figures 8 and 9) to two or three meters in the Carmine Bee-eater, the largest African species, and are dug in flat ground or in banks, especially by streams and rivers.

Rosy Bee-eaters (*M. malimbicus*) always nest in flat ground (Plate I). This is a rather dogmatic statement since we know of very few colonies; but so gregarious is this species that only extensive flat riverine sand bars are likely to suffice. During April and May, 1965, I canoed down the Kaduna and middle Niger Rivers searching for Rosy Bee-eaters, and found three colonies, all in wide, flat sand bars, the largest colony being 330 meters long and about 33 meters wide (Figure 2). Three randomly selected 10-meter-square quadrats contained 194, 220, and 241 nests, and allowing for incomplete and unoccupied nests, I estimated that the colony held at least 25,000 adult birds — a magnificent spectacle of slate and carmine filling the air with an overwhelming clamor. The other two colonies held about 8,000 birds each. I know of no other colonies of Rosy Bee-eaters found in Nigeria since 1946 (Brown, 1948), where I have explored about one hundred of the six to seven hundred miles of the Niger and Benue Rivers.

Red-throated Bee-eaters (*M. bulocki*) and White-fronted Bee-eaters (*M. bullockoides*) comprise a superspecies that inhabits woodland savannas (Figure 3), north and south of the equator, respectively, and are by contrast obligate cliff-nesters. Since their tunnels incline upward from the entrances they could not possibly construct them in flat ground. The tunnels of all bee-eaters end in an oval egg-chamber, which is unlined.

We know the breeding biology of the European Bee-eater in considerable detail (Rivoire, 1947; Swift, 1959). Despite its specialized nesting and feeding requirements, it will breed successfully in captivity if provided with earthen "cliffs." Koenig (1951, 1953) reported on detailed aviary studies of European and Large Green Bee-eaters. The following brief outline, taken from these sources, is representative of all *Merops* species.

## European Bee-eater

The European Bee-eater breeds colonially, in cliffs or flat ground. Burrows are about 1.5 meters long, the length varying inversely with the hardness of the substrate, and they take about 14 days to excavate. The birds loosen the soil with the bill and kick it out of the burrow backward with the legs. Within the confines of its tunnel, bee-eaters presumably work the legs alternately; but at the entrances of their nests I have commonly seen them support the body on a tripod of bill and wrists, enabling them to scrabble at the pile of loosened earth with both legs together (see Mountfort, 1957). On

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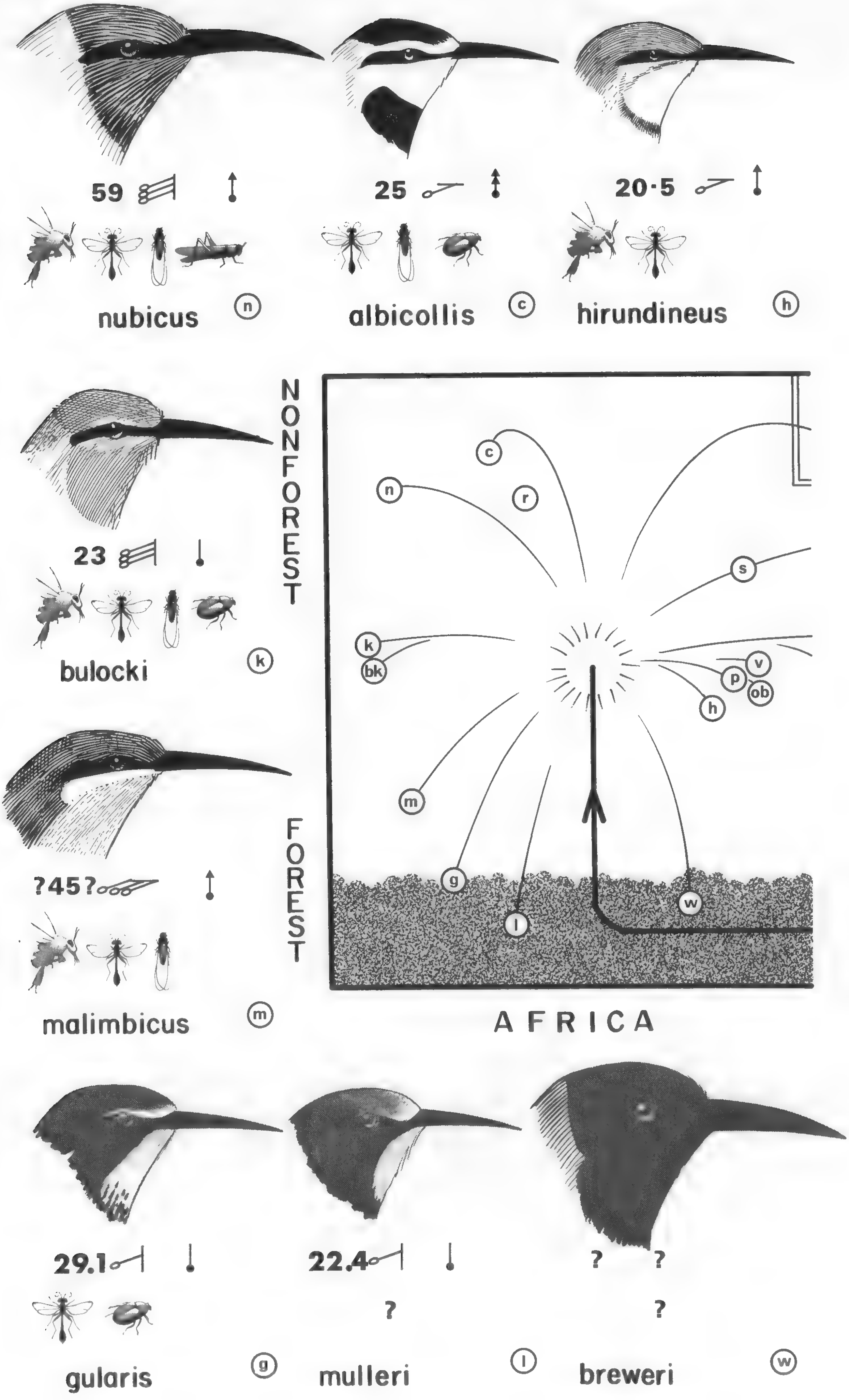
Figure 1 (*see following page*). A scheme for the evolution of the Meropidae, and biological data for some species. The family probably originated in Asian forest and radiated in African nonforest. The bee-eaters *not* illustrated are Blue-bearded, *Nyctyornis athertoni*, and White-fronted, *Merops bullockoides* (bk), Bay-headed, *M. leschenaulti* (ls), Cinnamon-chested, *M. oreobates* (ob), Blue-tailed, *M. philippinus* (ph), Somali, *M. revoilii* (r), Blue-breasted, *M. variegatus* (v), and Blue-throated, *M. viridis* (vd). The bill shape is precise. Refer to Figure 22 for an explanation of insect figures under staple foods. Here the termites represent termites and ants. The mean weight is in grams. Nesters in flat ground or cliffs can be solitary, one tunnel; aggregate, two tunnel; or colonial, three tunnel. A bar means sedentary; an arrow signifies migratory. The number of arrows indicates the extent of migration.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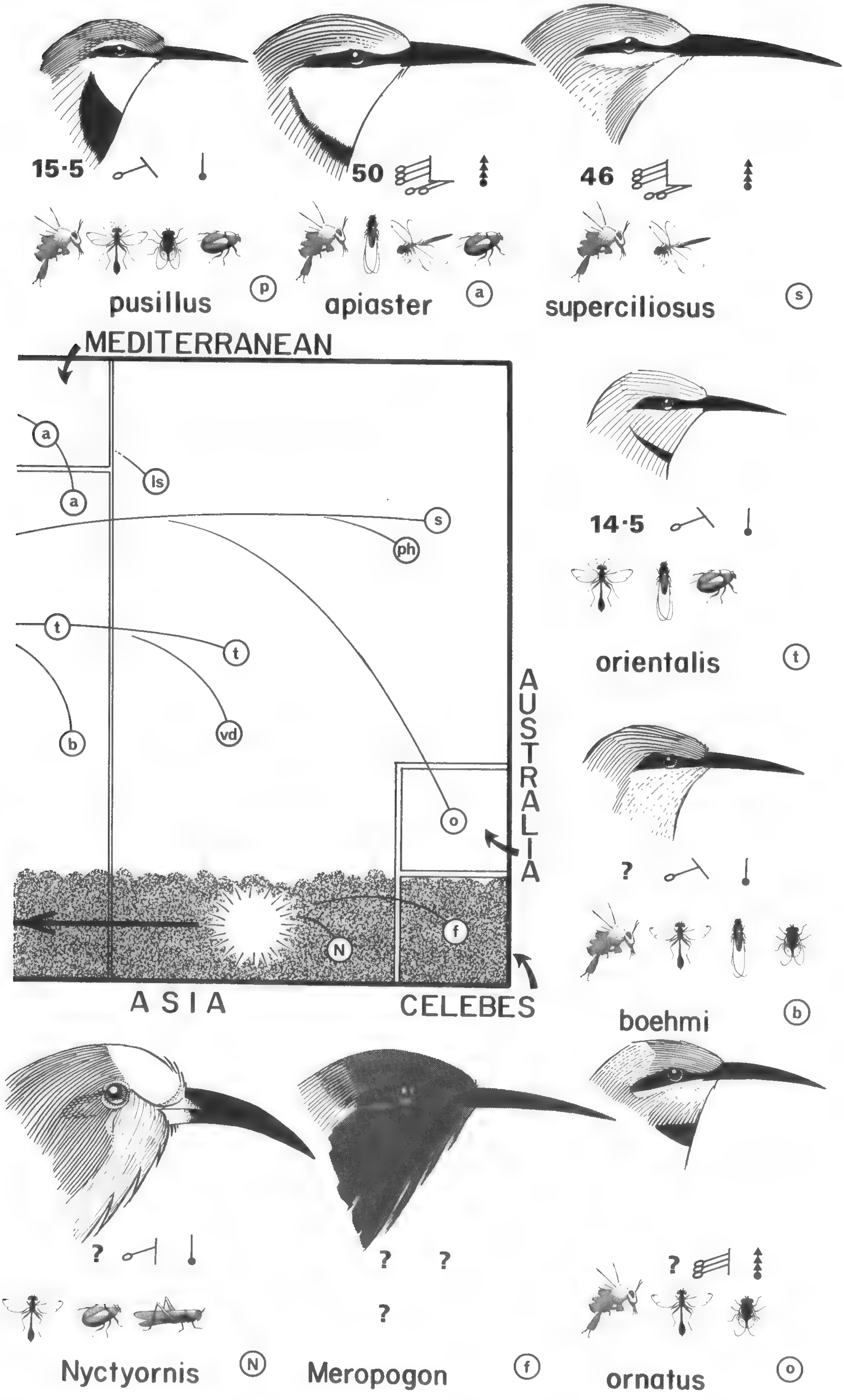
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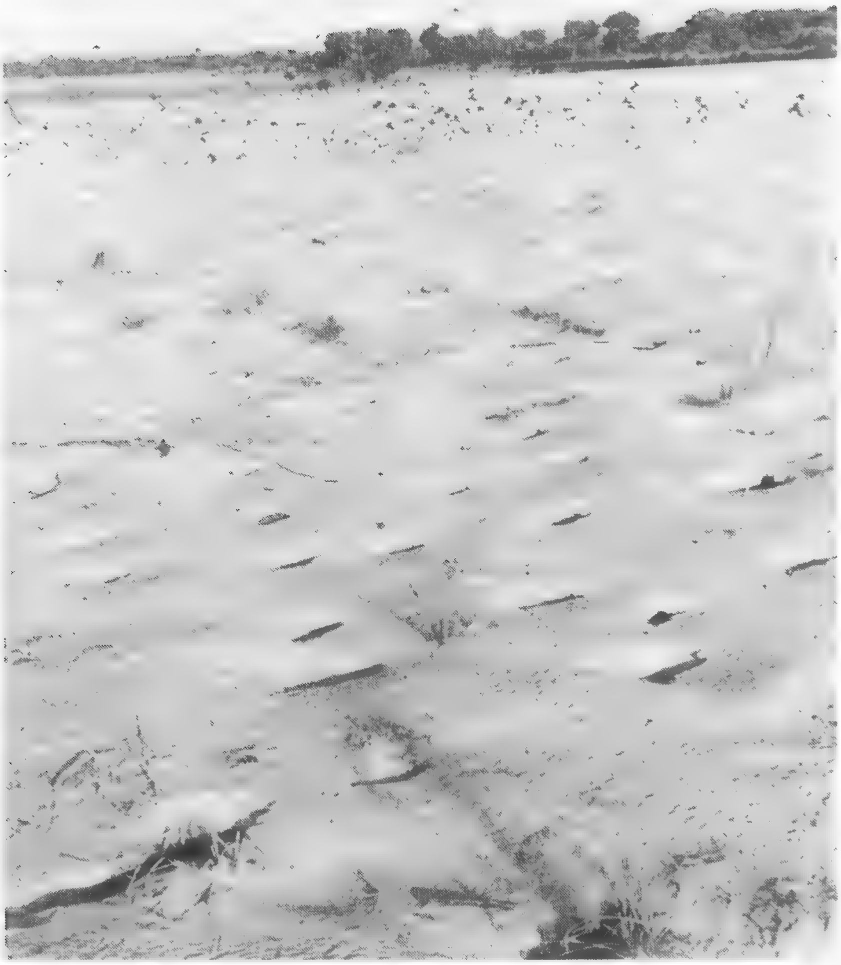


Figure 2. Part of a huge colony of 25,000 Rosy Bee-eaters. This colony, in a sand bar in the Niger River, Nigeria, is one of the few ever discovered.

arrival in Europe from African wintering grounds, the pair-bonds are already established. When a pair has chosen a site or hole, it starts to defend one or more nearby perches and the immediate vicinity of the nest entrance.

Courtship is not elaborate; an upright stance adopted by partners prior to copulation is often followed by ritualized insect-beating movements by one bird against the perch at the other's feet. Courtship feeding begins with nest excavation, and later on it often precedes copulation. In all bee-eaters, the sexes have similar plumage. Koenig (1951) showed postures of female European Bee-eaters soliciting copulation, in passive and active threat, and fighting. Both sexes excavate, incubate, and feed the young. The female lays from four to seven subspherical white eggs at intervals of one or two days; the clutches in tropical bee-eaters are smaller, two to five eggs. Incubation begins with the first egg and lasts for 20 to 26 days after completion of the clutch. During the incubation period a very marked social hierarchy develops within the colony, dominance being exhibited by aggressive side-stepping (*Seitwärtstrippeln*) postures.

The young hatch at one- or two-day intervals and are altricial, a conspicuous character being the swollen heel-pads they rest on. By this time the nest chamber has acquired a blackish litter of insect sclerites — hard chitinous pieces of integument — which are regurgitated by incubating and roosting adult birds as compact pellets about two centimeters long. As the young grow, the litter becomes deeper and the sides of the nest chamber are encrusted with dried excreta, for the adults do not remove the fecal sacs. With the decomposition of uric acid, the nest acquires a powerful stench of ammonia, which clings to the adult birds for several hours after visiting the nest. With the opening of the eyes at about eight days of age, the demand for food by the young becomes more insistent and growth accelerates. Four different begging calls develop progressively. The young fledge at about 30 days of age, and the prey-beating behavior matures at fledging.

## Red-throated Bee-eater

The Red-throated Bee-eater is the species that I have studied the most intensively (Figure 4). At Zaria, 11° 10′ N Lat., 7° 40′ E Long. in woodland savanna in northern Nigeria, I banded the majority of birds in several colonies and followed their history from 1964 through 1967. I also devised a successful method for direct observation of the birds in the nest chamber (Fry, 1972).

### A Site for Survival

Colonies generally comprise about 60 birds, with the extremes at Zaria being 9 and 110. The birds abandon many tunnels before completion, so the average number of perforations in the cliff face is nearer 50 than 30 — all within about one square meter. It is hardly surprising that such undermined cliffs often collapse, but this is more prone to happen during the rainy season, after breeding has been completed. All the same, tragedies do occur and an entire colony of birds can perish overnight.

Most bee-eater species nest in cliffs (Figure 5) or in flat ground but not in both, although at least four species habitually use both: the Large Green Bee-eater (Marien, 1950), the Bay-headed Bee-eater (*M. leschenaulti*) of Asia (Cairns, 1957), the Carmine Bee-eater (Koenig, 1956; Figure 4), and the European Bee-eater.

The great disadvantage of riddled cliff sites collapsing is offset by their relative safety from predators. Another advantage of nesting in cliff faces

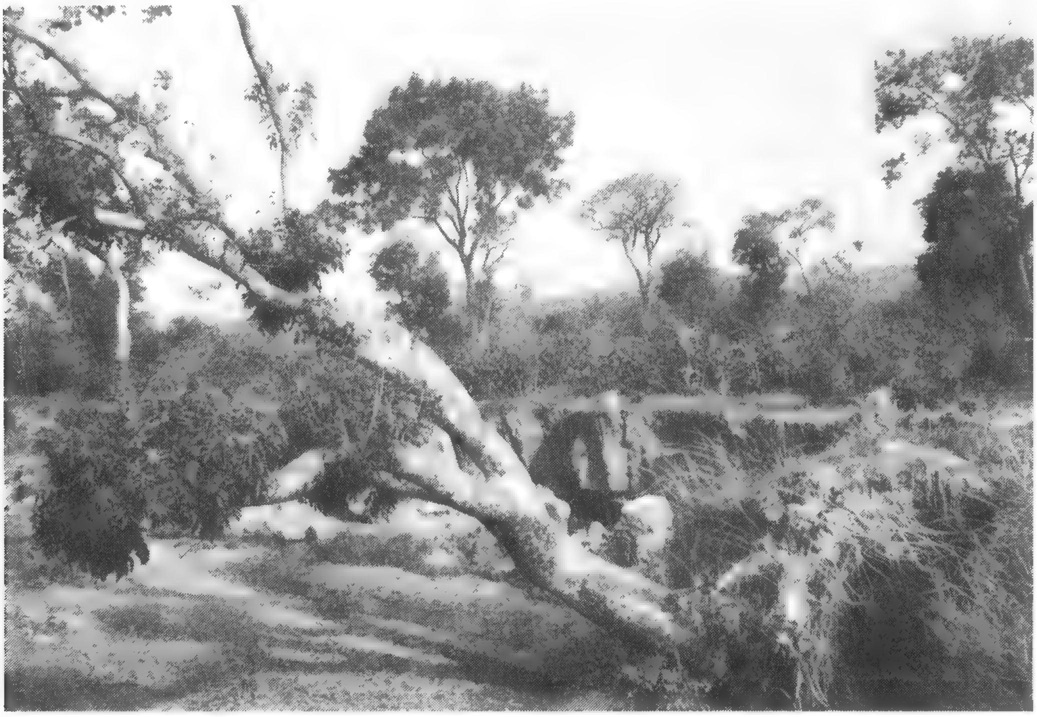


Figure 3. Typical habitat of Red-throated Bee-eaters. Photographed at Zaria, Nigeria.

rather than in flat ground is that damage from rain and blowing sand is lessened. However, in Red-throated Bee-eaters, despite a hump in the nest tunnel (Figure 6:3), up to five per cent of the eggs are lost by accidental ejection, something which could not possibly occur in flat-ground nesters.

There are other causes of mortality. In a small colony of White-throated Bee-eaters (*M. albicollis*; Plate II) nesting in flat ground near Lake Chad (Figure 7), a sandstorm entirely obliterated the colony and all entombed birds died. Bee-eaters nesting in flat ground are fair game for numerous predators, from snakes and lizards to honey-guides and viverrines (cat-like mammals of the family Viverridae). Monitor lizards (*Varanus* spp.) will even climb low cliffs to dig away the face and eat the exposed eggs or young birds. Not even Red-throated Bee-eaters are safe from the egg-eating snakes (*Dasypeltis*), which can sometimes climb down from the top of the cliff, using projecting roots. One of the safest places for nest holes is perhaps the roof of the half-meter-wide tunnels of aard-varks (*Orycteropus afer*). Least Bee-eaters use them wherever aard-varks are common (Figures 8 and 9).

A frequent cause of death in all bee-eater nest holes is an adult accidentally wedging its head sideways and being trapped in the narrow tunnel. Any nestlings or other adults in the nest chamber at the time also perish. Another major cause of mortality is honey-guides. Like cowbirds and cuckoos, they are brood parasites, specializing on hole-nesting birds. Greater Honey-guides (*Indicator indicator*) parasitize a high proportion of bee-eater nests; Lesser Honey-guides (*I. minor*) parasitize small bee-eater species. On hatching, the young honey-guide is equipped with needle-sharp hooks on the upper and lower mandibles, which it uses to lacerate and kill the newly-hatched bee-eaters. Other predators of bee-eaters include man, a snake (*Malpolon monspessulanus*), and a lizard (*Lacerta lepida*) in Europe (Swift, 1959), and two falcons — the Lanner (*Falco biarmicus*) and Hobby (*F. cuvieri*) in Nigeria. Clapham (1964) found that Large Green Bee-eaters are the commonest prey of Sooty Falcons (*F. concolor*) in the Red Sea in autumn.

Red-throated Bee-eaters excavate their holes in relation to the top of the cliff; whatever its height — generally 1.5 to 8 meters — nest entrances are about 25 to 250 centimeters from the top. Digging starts toward the end of the wet season, about the end of September at Zaria, and continues for short periods at dawn and dusk until the terminal chamber is large enough to roost in. At this time of year the earth is moist, but as the dry season progresses, it dries out to a concrete-like hardness making digging very difficult. Bee-eaters begin to roost in their nest holes when periodic dust-laden winds from the Sahara bring cold nights, but they do not initiate breeding for nearly four months.

## Displays

A greeting or recognition display, which commonly occurs throughout the year in Red-throated Bee-eaters consists of excited trilling by both birds when one alights near another already perched, and is accompanied by fanned and vibrated tail, slightly raised crest and upright stance, the birds facing each other (Figure 10:1). The intensity varies and, when a bird alights on the face of a breeding colony, several others may also give a high-intensity display which may terminate in aggression and flight.

Courtship behavior develops from this greeting display. When still in an upright stance with vibrating tail and calling, both birds rapidly bob the head in such a way that the tips of their bills are nearly or actually touching

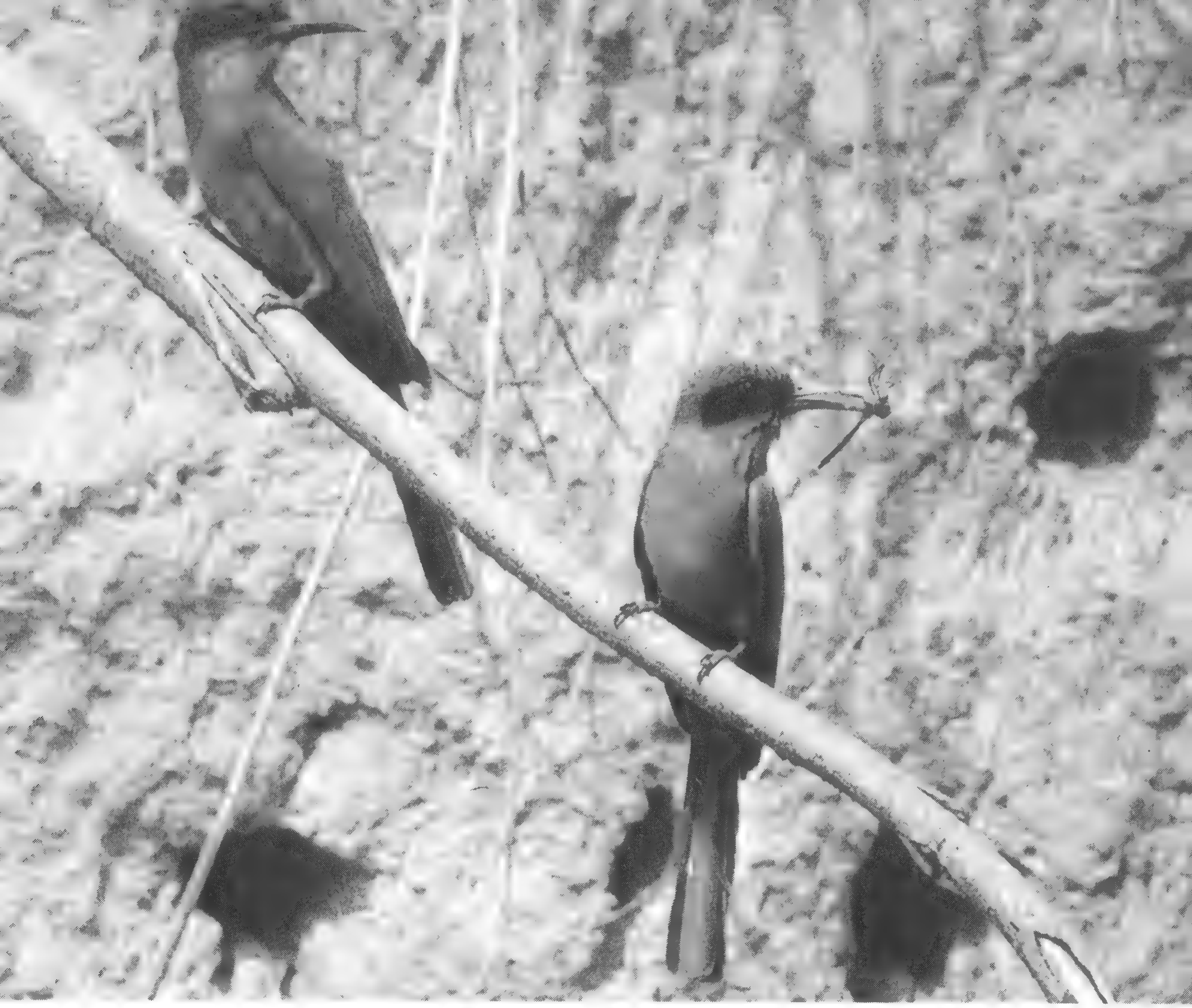


Figure 4. Red-throated Bee-eater. Pair of adults outside cliff nests, Zaria, northern Nigeria.

(Figure 10:2). I saw nothing in the behavior of the Red-throat comparable to the upright position phase of courtship — *Balzruckstellung* — described and illustrated in the European Bee-eater by Koenig (1951).

The courtship displays of other African species also vary a good deal, but they all contain an element of head-bobbing which seems to be derived, phylogenetically, from the all-important prey-deactivating behavior described below. Indeed, White-throated Bee-eaters incorporate a "bee-rubbing" sequence — without a bee — into their display as a prelude to courtship (Figure 10:4), and the behavior corresponds exactly with functional bee-devenoming. During courtship in Carmine Bee-eaters, the birds bow the head a number of times in rapid alternation (Figure 10:6), the bill nearly striking the perch at the partner's feet. Koenig (1953) regarded a similar occurrence in European Bee-eaters as ritualized insect immobilization, given as a displacement activity prior to copulation. But in Carmines it is too regular an event to be regarded merely as a displacement activity and, in fact, seems to be a prerequisite to copulation. I should note, however, that bee-rubbing is not an uncommon vacuum activity in many bee-eaters under other circumstances. In the Rosy Bee-eater, the component of ritualized insect-beating, retained in courtship, has been reduced to jerking the bill upward to alternate sides through a small arc (Figure 10:7).

White-throated Bee-eaters, which have a more strikingly pied plumage than other species, also have the most elaborate displays. A high-winged glide, alternating with unusually shallow wing-beats, may be described as "butter-flying." The bird has an unusually deep-chested appearance and the flight is accompanied by vociferous calling, which terminates in a perched greeting ceremony like the Red-throat's, but with raised wings (Figure 10:5). It may signal courtship, when the bird folds the wings, raises the crest high, and bobs up and down on flexed legs (Figure 10:3), alternating with bouts of ritualized bee-rubbing.

## Cooperative Breeding

Egg-laying by Red-throated Bee-eaters in early February is heralded by renewal of excavating, some tunnels being dug anew, others spring-cleaned. It is a time of excited activity at the breeding site. Watching individually marked birds, I soon discovered that any one bird will enter many nest holes in quick succession and that several of the nests have more than two adults in regular attendance. What at first appeared to be a promiscuous situation has in part resolved itself (Fry, 1972), although we must know very much more before we can interpret the extremely complex social organization of bee-eaters. About one-third of the nests in a colony of Red-throated Bee-eaters proved to have a number of helpers, varying from one to three, attached to the parents. The helpers' bonds, formed well in advance of the breeding season, remain more tenuous than the pair-bond between the parents. However, all bonds seem to be reinforced during the breeding season, with the helpers assisting in excavation, incubation, and provisioning; and the helpers, which are mostly males, may even copulate with a parent. It is thus impossible to establish in all cases which of the several males that attend a nest is the father of the brood. Generally there is not much doubt about it, since one of the males is pre-eminent in all reproductive responsibilities.

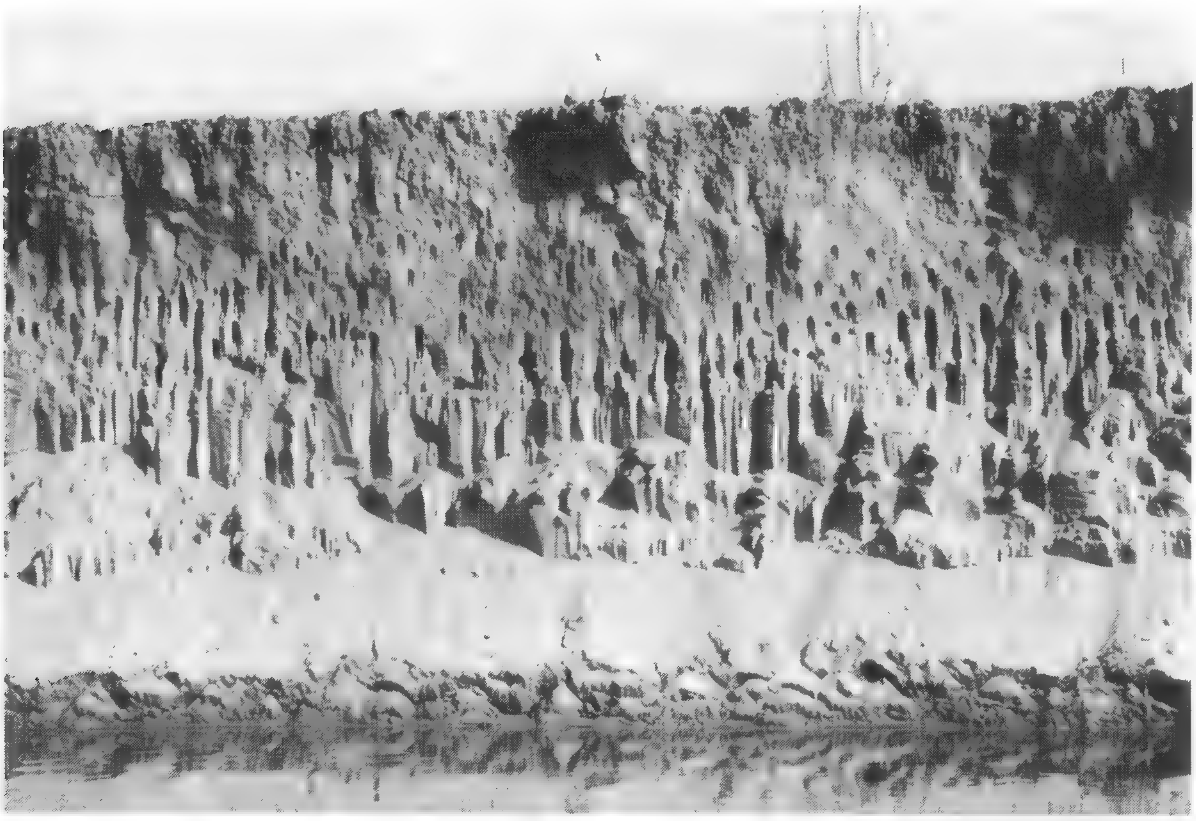


Figure 5. Part of a colony of Carmine Bee-eaters with a few nests of Red-throated Bee-eaters on the Kaduna River, Nigeria.

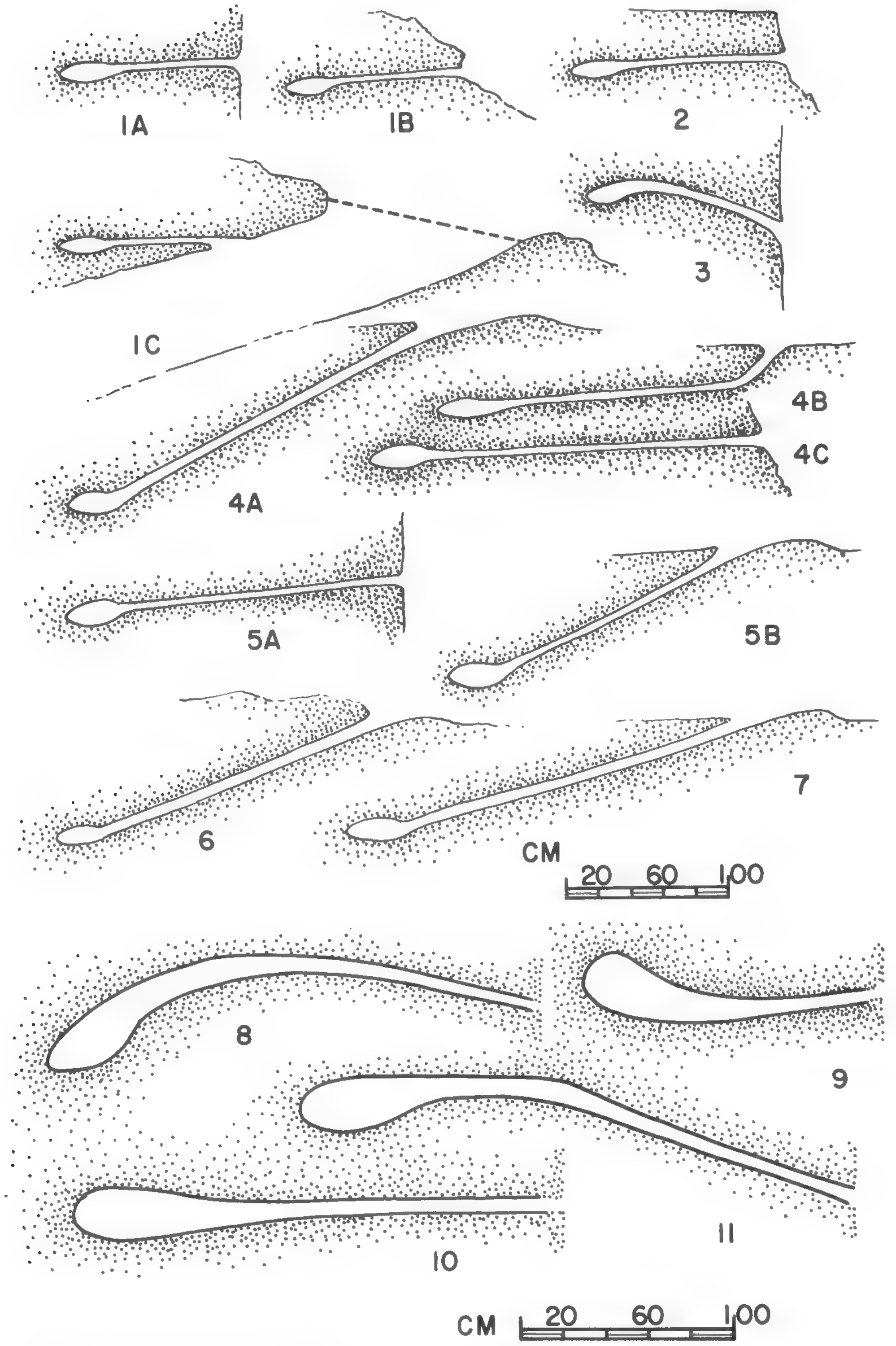


Figure 6. Nest profiles and plans. Profiles: 1a–c, Least Bee-eater (1c in roof of an aard-vark burrow); 2, Little Green; 3, Red-throated and White-fronted; 4a–c, European (redrawn after Swift, 1959); 5a–b, Large Green and Carmine Bee-eaters; 6, White-throated; and 7, Rosy Bee-eater. Plans: 8–11, four common shapes that appear to be non-specific.

All of the colony-nesting savanna bee-eaters seem to have helpers at the nest, with as many as five helpers found at one nest of White-throated Bee-eaters. Some of the helpers are last year's offspring of the pair they assist, and this may prove to be the rule. I also found that there is a preponderance of males in the gregarious bee-eaters, about one-and-one-half males per female in the Red-throated, European, and Carmine Bee-eaters, and a rather higher proportion in the White-fronted and White-throated Bee-eaters. Solitary-nesting species, such as the Least Bee-eater and Blue-breasted Bee-eater (*M. variegatus*), have an equal sex ratio and appear not to have any helpers at the nest.

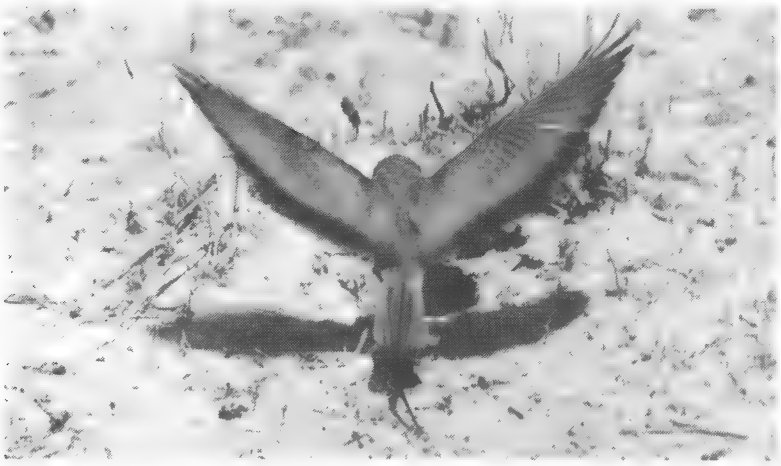


Figure 7. White-throated Bee-eater alighting at its nest near Lake Chad. The nests are often excavated in the lee of a piece of vegetation, as here.

Since Skutch (1961) reviewed the subject of helpers at the nest, many more cases have come to light, all in hot climate species. Now we know of at least 60 species from broad systematic and ecological spectra, in the tropics and other perennially hot environments, with a cooperative breeding and social organization in many cases very much like that among bee-eaters. I suggested (Fry, 1972) that the system provides a reserve of experienced apprentices whose subsequent recruitment to the breeding pool is a means of population regulation in both seasonal and relatively non-seasonal habitats.

## Eggs and Young

Red-throated Bee-eaters in Zaria lay up to four eggs at daily intervals in the midmorning; the mean clutch is 2.4 (Figures 11 and 12). I have not measured the incubation temperature. With nest tunnels one meter long, the egg chamber is sufficiently protected to have a relatively constant temperature. At the hottest time of day, the greatest temperature on the cliff face was 50.5° C, the air temperature was 38.5° C, the shade temperature 35.4° C, and the egg-chamber 32.0° C. Any cooling at night is largely offset by the body heat of parents and helpers which crowd into the nest to roost.

Both parents incubate and the helpers may assist; the incubation period is between 20 and 21 days. Since incubation begins with the first egg, hatching is at daily intervals and the size range among the young remains quite distinct until fledging. Figure 13 shows that the older bird in each of the broods of two young maintained an even growth rate until the maximum weight was reached about the 20th day, while the younger bird in each brood showed a marked decrease in growth rate at about the 8th day. At that time, the older sibling became markedly more mobile, shuffling backward and forward with equal ease on its heel callosities, and was the first to meet the adult coming in with food. The adults bring only one meal at a time, a single insect, and feed only one nestling. The older bird is thus assured of the lion's share of the daily fare, and sometimes the younger one, failing to get enough food, dies early in its second week.

Fledging occurs about the 28th day, but in any one brood the older nestlings achieve their maximum weight a few days before fledging. About the 20th day, their average weight is around 28 grams at 3:00 PM — maximum recorded 31.5 gm — considerably in excess of the mean adult weight of 23.9 gm at the same time. The last week in the nest is a period of development rather than growth with (1) an irregular decline in weight of at least the older nestlings, resulting from a rejection of many proffered meals, (2) a regression of liver and gizzard sizes (Table 1), and (3) the mobilization of fat reserves. Reduction in gizzard weight may well be related to the change in diet from large non-venomous insects before fledging to smaller venomous ones afterward.

There is no distinct juvenal plumage in bee-eaters; the young birds' plumage is like the adults'. For some weeks after it has fledged, the young bird can, however, be distinguished with ease by its fresh, unworn, and unbleached plumage and shorter tail and bill. For a few days at least, its behavior remains decidedly juvenile — particularly its inept handling of stinging bees.

The Meropidae is one of the few families which postpones the postnuptial molt until completion of any migration after breeding. In the sedentary Redthroat the postnuptial and postjuvenal molts start four weeks after the time of fledging. The molt of primaries and of secondaries is centrifugal — away from the body — but the proximal three or four primaries are shed at the same time or very nearly so. Thereafter the distal primaries are replaced outwardly one by one over a period of eight weeks, so that the aerodynamically important distal end of the wing is never without a nearly full complement of remiges.

## Breeding Seasons

Nigeria is particularly well placed for studies of bird biology in relation to climate because there is but a single rainy season each year, its duration varying inversely with distance inland, or northward. Near the coast, in an east-west belt of lowland rain forest, rain falls throughout the year, with some diminution about December and January. The rain forest is bordered on the

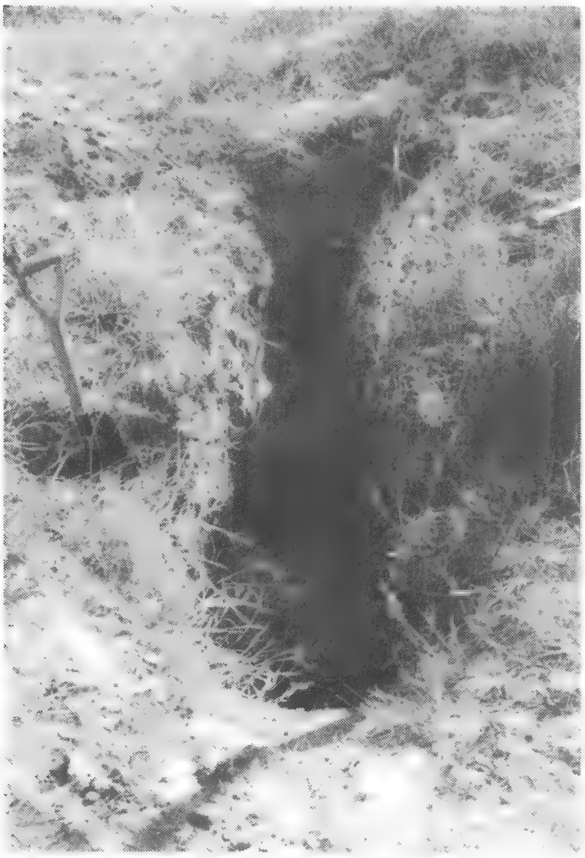


Figure 8 (*left*). Least Bee-eater nest excavated in the roof of an aard-vark burrow, Rhodesia.

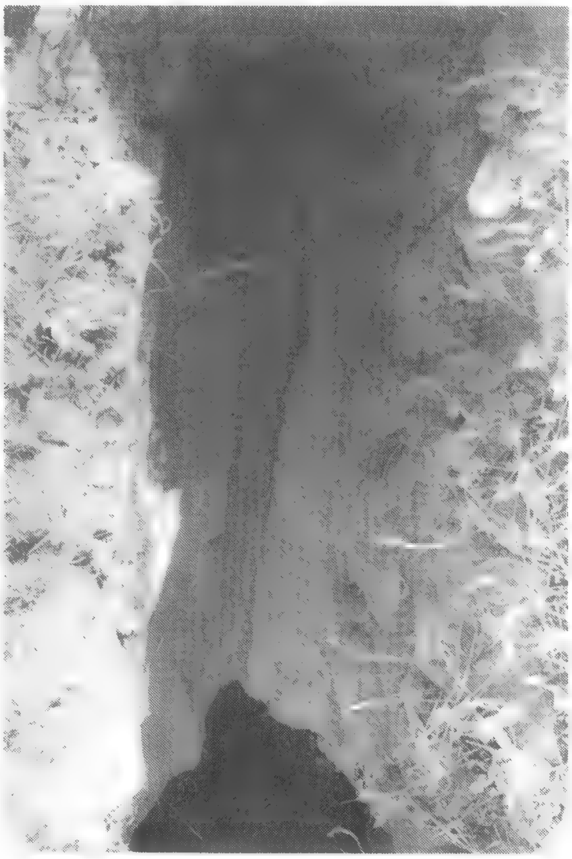


Figure 9 (*right*). A closer view of the nest tunnel and chamber in the photograph at left.

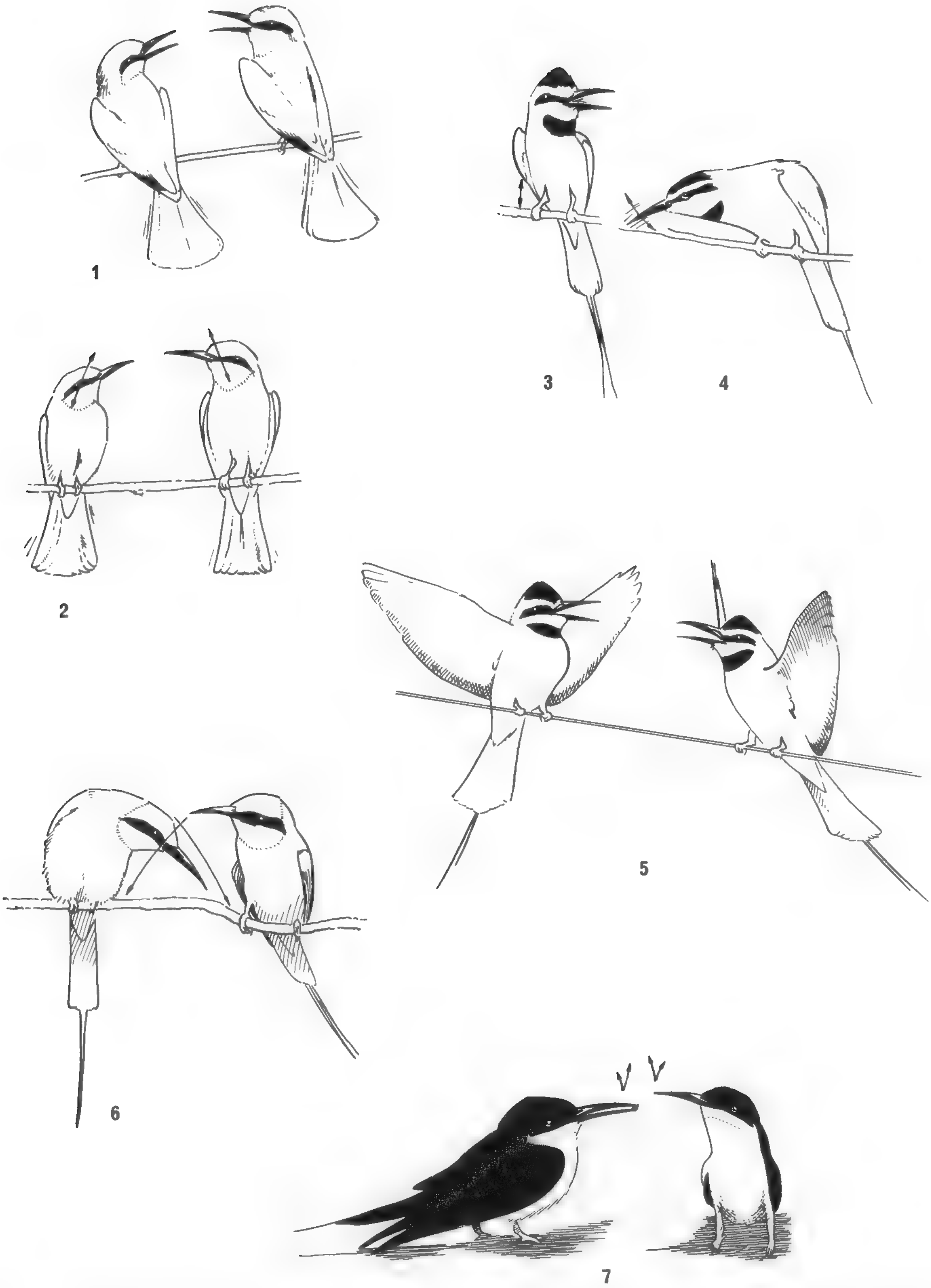


Figure 10. Some displays: (1) High-intensity greeting and (2) head-bobbing courtship in Red-throated Bee-eaters; (3) leg-bobbing, (4) ritualized "bee-rubbing," and (5) high-intensity greeting (pre-copulatory) in White-throated Bee-eaters; (6) head-bobbing in Carmine Bee-eater and (7) in Rosy Bee-eater.

TABLE 1

Weights in Grams of Organs of Red-throated Bee-eaters

| *Age in days* | *Whole bird* | *Empty gizzard* | *Liver* |
|---|---|---|---|
| 4 | 8.8 | 1.4 | 0.2 |
| 5 | 9.2 | 0.9 | — |
| 6 | 12.5 | 1.8 | 0.6 |
| 7 | 14.6 | 2.1 | 0.6 |
| 9 | 18.4 | 1.8 | 0.7 |
| 11 | 20.7 | 2.0 | 1.1 |
| 11 | 20.8 | 1.5 | — |
| 12 | 21.3 | 1.5 | — |
| 14 | 23.1 | 1.4 | — |
| 18 | 24.4 | 1.7 | 1.0 |
| 21 | 27.1 | 2.2 | 1.2 |
| Adult | 22.6* | 0.79*<br>S.D.=0.065 | 0.69*<br>S.D.=0.065 |

*Means of 20 birds.

north by "Guinea" woodland savannas, determined by a climatic regime with a few months of greatly reduced rainfall, almost drought. Still farther to the north there is an east-west zone of "Sudan" savanna, dominated by an uninterrupted drought of over seven months. The next northerly vegetation zone is "Sahel" savanna, under drought for nine or 10 months, with rains and a short growing season in July and August.

The coastal forest and adjacent moist woodland savannas are not very seasonal and probably provide an abundance of food and other resources for birds throughout the year. But the farther north one proceeds through various vegetation zones, the more seasonal the climatic regime becomes, with a prolonged drought in sub-Saharan latitudes that must be every bit as inimical to life for most birds as is the temperate zone winter. Consequently, many native birds migrate, particularly in the more arid habitats, and the bee-eaters are no exception (Elgood, Fry, and Dowsett, in press).

Most African savanna bee-eaters breed early during the rains, fledging their young in a given latitude when the rains are well advanced and when there is plenty of insect food available. None of the species has more than one brood a year. Of seven Nigerian savanna bee-eaters, all nest during the rains except the Red-throated and the Little Green, both of which breed in the late dry season. Figure 14 shows that the fledging times of the others are concentrated into a time-space triangle corresponding with the pattern of rainfall. Some bee-eaters, like the Least and the Carmine, range widely, breeding in all savanna zones. As a rule in each such species, nesting takes place later at successively higher latitudes; at the southern edge of the Nigerian range of the sedentary Red-throated Bee-eater, for instance (at 8° 30′ N Lat. on the

Ogun River), all nests held completed clutches at the end of January while at the most northerly colony found in Nigeria (at 12° 53′ N Lat. near Kaura Namoda), the young were only about 10 days old at the beginning of April.

In more southerly latitudes in Nigeria where the rains last for several months, the various bee-eater species at a given locality breed at different times and seem to apportion the favorable wet season between them. Carmine and Least Bee-eaters, the largest and nearly the smallest of the savanna bee-eaters, nest at the same time, and, despite the similarity of their diets, may effectively avoid competition by consuming different size ranges of the same prey species. Farther north, the brevity of the wet season obliges all the bee-eaters to nest about the same time.

Even when the nesting seasons of several species at one latitude are not the same, there must still be considerable competition for food arising from the fact that large numbers of prebreeding or postbreeding bee-eaters of other species are present. On the middle Niger River, Red-throats fledge in the first half of April, Carmines and Leasts in the second half of May, Large Greens in early July, and Rosy Bee-eaters in late July. But in May, one square kilometer contained hundreds each of Red-throats, Leasts, and migrating White-throats, and thousands of Carmines and Rosy Bee-eaters (Figure 15). No Large Green Bee-eaters nested locally the year I was there. Figure 15 shows a number of feeding stations. The competition for food which results does not compare with, say, a field in Europe that provides food for four species of wintering thrushes, since many bee-eater species occur abundantly in the one habitat throughout the year. One is forced to speculate as to whether the moist tropical woodlands do not provide an abundance of food for many bird species the year round.

## *Migration*

Studies of banded birds at Zaria showed that Red-throated Bee-eaters are entirely sedentary there. Individuals seldom wander more than a kilometer or two from the stretch of stream bank where they nest. There is some evidence, however, that marginal populations of this and other sedentary bee-eaters, such as the Least and Black, are migratory.

By contrast, the European Bee-eater is an intercontinental migrant; it breeds north to about 54° N Lat. and winters in tropical and southern Africa, a movement in the species' center of abundance of 6,500 km. Migration of some populations of Large Green Bee-eaters and of the sibling Blue-tailed Bee-eaters are equally distant, while the Rainbow-birds move between Australia and New Guinea. The farthest intracontinental migrant is the White-throated; it breeds about July in sub-Saharan steppe and winters in the moist woodlands around the equatorial forest, south to about 5° S Lat. — a mean migration rather over 1,000 km.

Between these extremes, bee-eaters exhibit every degree of migration (Elgood, Fry, and Dowsett, in press). All bee-eaters migrate by day and are very conspicuous. In Africa, the migrations are generally synchronized with the movements of the inter-tropical front, and operate so that the migrant population stays in much the same climate throughout the year.

## *Voices*

All of the bee-eaters, both solitary and gregarious species, are vociferous in and out of the breeding season. Eleven different voices have been detected

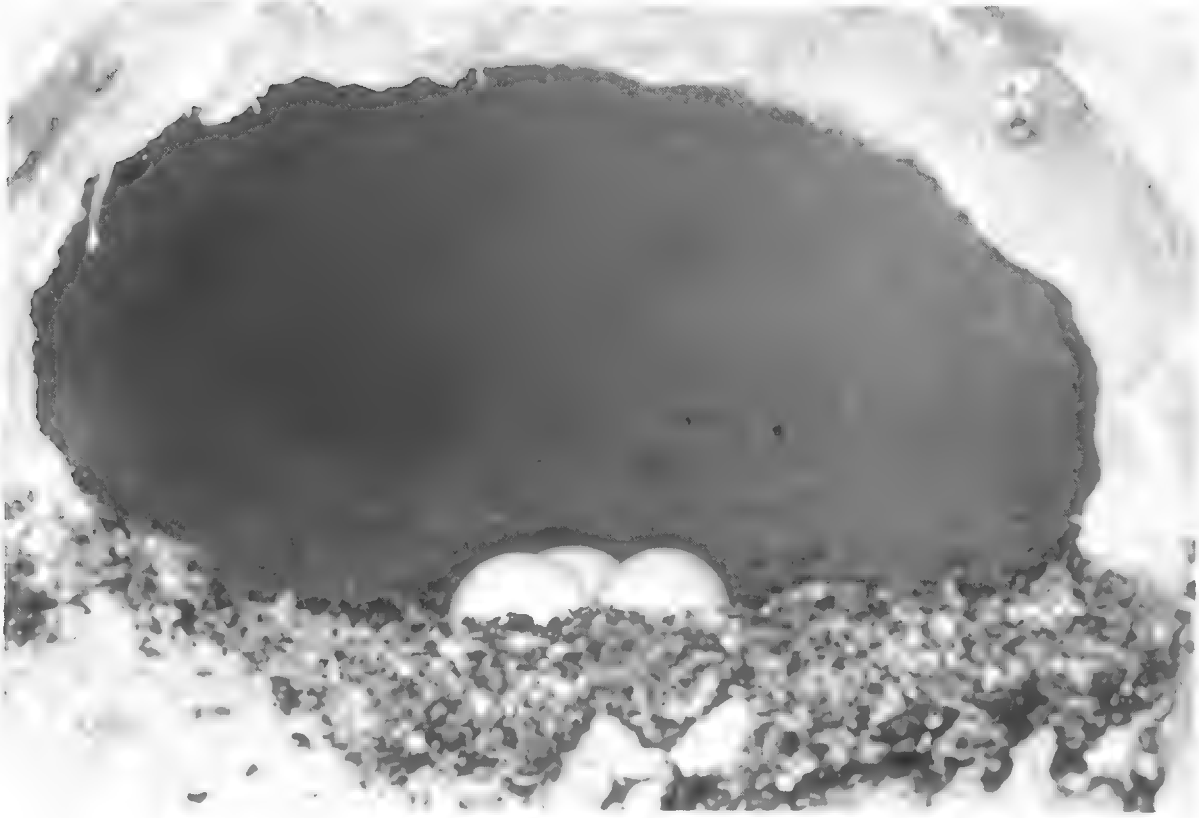
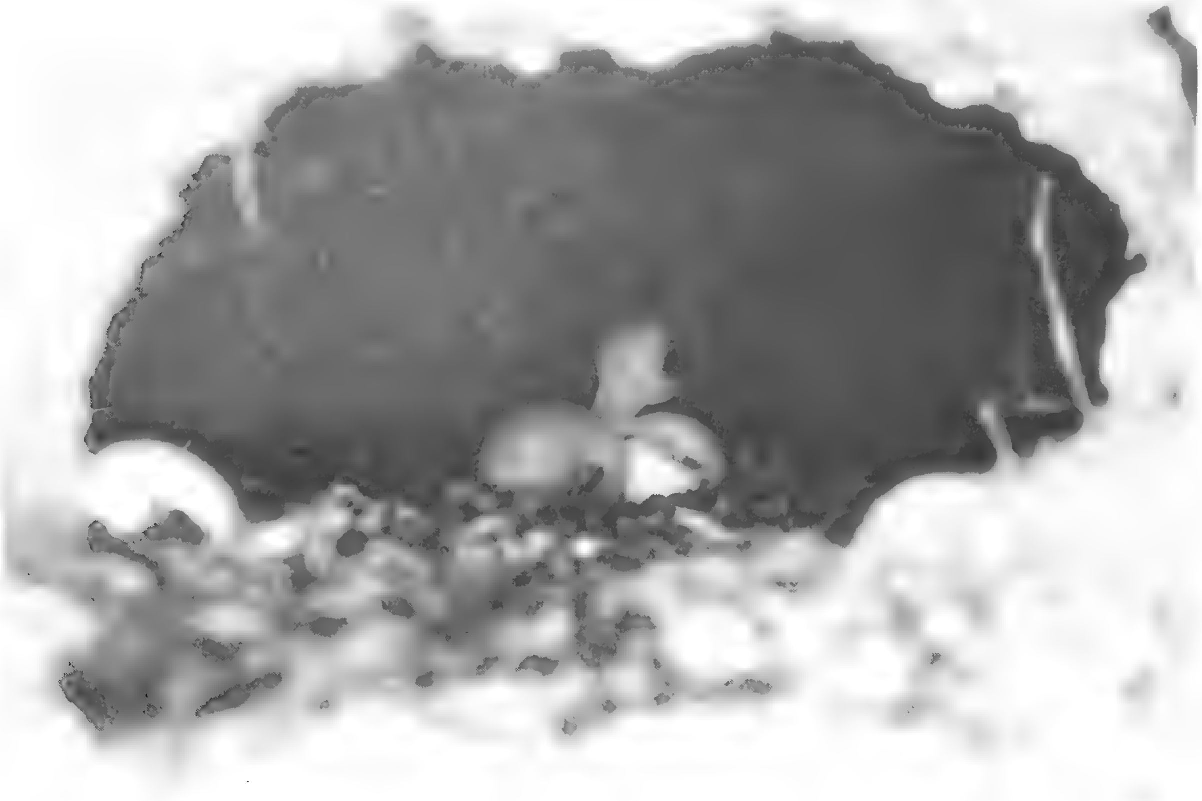


Figure 11 *(above)*. A clutch of three white, unmarked eggs in the nest chamber of the Red-throated Bee-eater.

Figure 12 *(below)*. A day-old nestling of the Red-throated Bee-eater. Both views were taken from an inspection trench (see Fry, 1972, Figure 1) looking toward the entrance tunnel, the inner end of which is clearly visible in the upper photograph.



in Red-throated Bee-eaters, almost as many as in European Bee-eaters (Swift, 1959). The Red-throat's calls are:

1. Perched call, low intensity: *wip.*
2. Flight call, low intensity, similar with terminal inflection; high intensity: a loud *weep, wit . . .*
3. General excitement, flight intention, low intensity alarm: a chattering *trrrrr-ic;* at higher intensity a *chur* with a slight cadence.
4. Alarm: *tirri-tee-tee.*
5. Greeting: an excited trilling *trrrr-treee trr trr tru.*
6. Roosting intention: a single plaintive low-pitched *pee-ouw* or *prre-ow.*
7. Copulation: a muffled sound difficult to represent phonetically; given also inside nests, perhaps during copulation.
8. Food delivery to mate: *chuf . . . chuf . . . chuf.*
9. Food delivery to juvenile: *prrp.*
10. Begging by nestling: *seep.*
11. Advanced nestling and juvenile soliciting food: a persistently reiterated *weep* or *wirrp.*

In the southern tropics of Africa, the White-fronted is a close relative of the northern Red-throated Bee-eater. Although the two are so similar in plumage that they have often been regarded as comprising a single species,

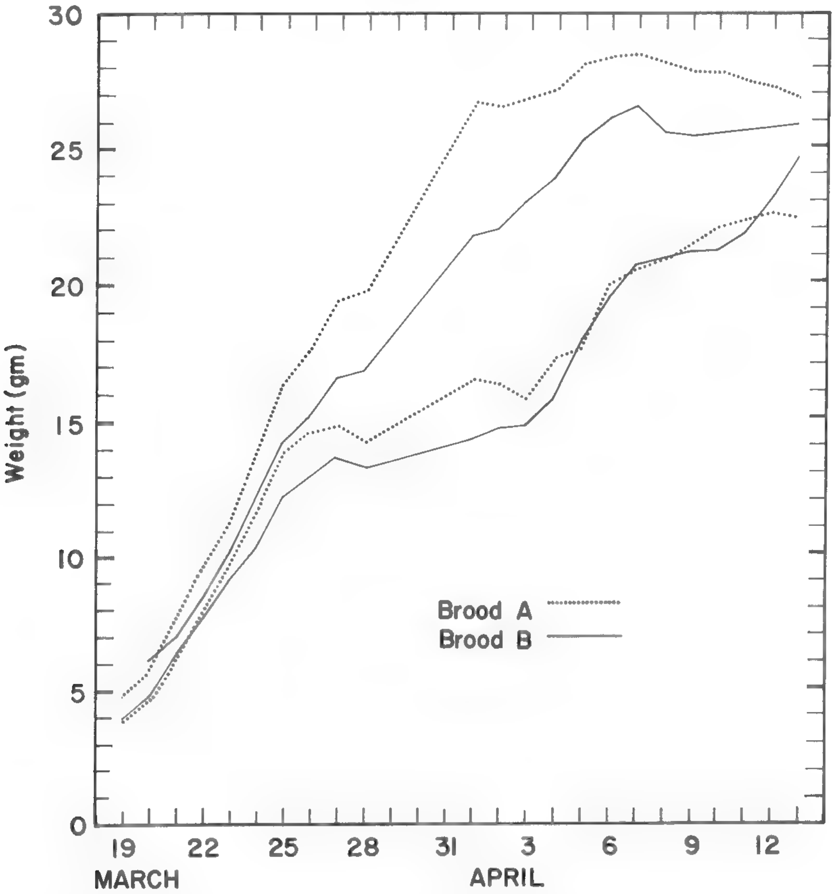


Figure 13. Growth curves for two broods of Red-throated Bee-eaters, each with two nestlings hatched on 17 and 18 March. Note how the growth rate of the younger siblings begins to fall about its eighth day, when the older one becomes sufficiently mobile to seize most incoming provisions. Data are from running averages of three consecutive day-weights; but no weights were taken on 29 through 31 March.

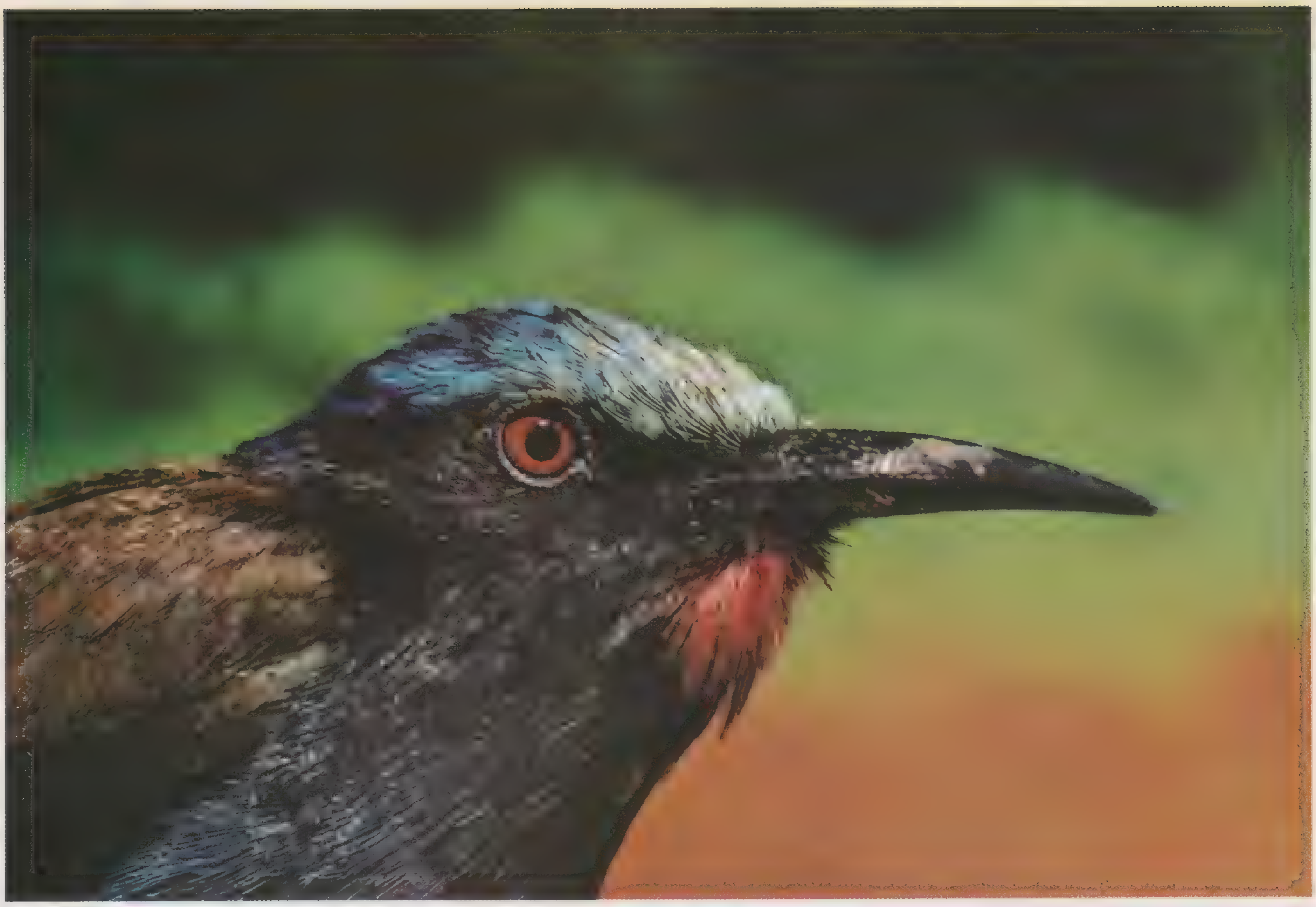
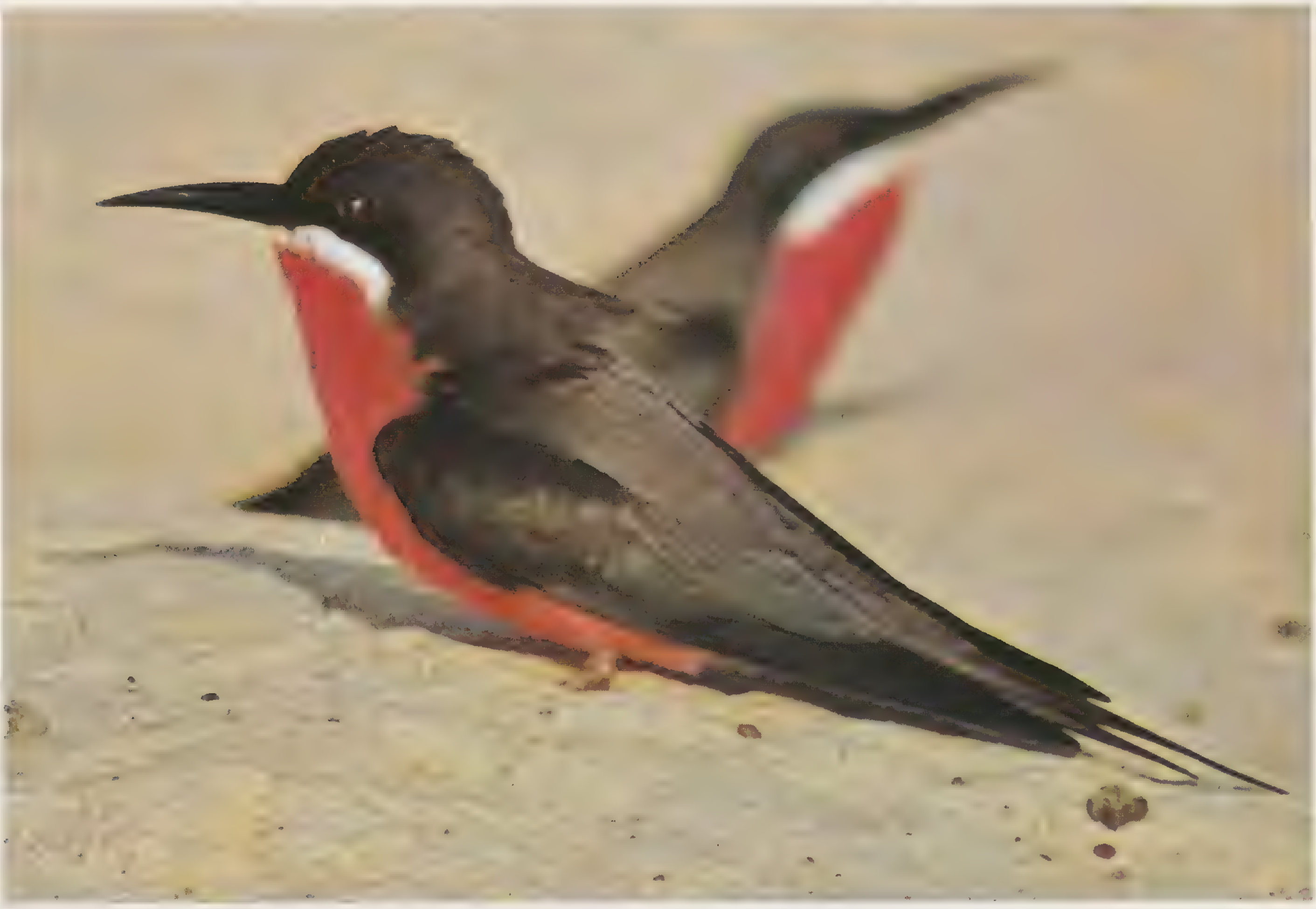


Plate I. *Above,* Blue-headed Bee-eater, *Merops muelleri.*
*Below,* Rosy Bee-eater, *Merops malimbicus.*



they differ in such characters as size and voice. White-fronteds are about one-and-one-half times as heavy and their voice differs greatly in quality, being deeper in pitch and slightly nasal. Their low intensity flight call, unlike the soft *weep* of the Red-throat, is a guttural *(g)eeauu* or *gaa-uc*. It is still possible to recognize all the White-front's expressions as having an affinity with those of its relative.

The voices of most other species that I have heard are rather similar in quality and range to the voice of Red-throats. Least Bee-eaters and their close relatives, Swallow-tailed Bee-eaters (*M. hirundineus*), Blue-breasted Bee-eaters, and Cinnamon-chested Bee-eaters (*M. oreobates;* Plate II), all have call notes like *wic* or *ti . . . ti;* they also have a "song," a pleasant, quiet jumble of notes derived from the call notes — a rapid *teu-teu-tiri-teu,* and Swallow-tails have a rolled component reminiscent of some larger *Merops* — a liquid treble *pee-ee-pirri-pree.* Flight calls and other calls of the Rosy, European, and White-throated Bee-eaters are all very similar. Very different from other African bee-eaters are the voices of Carmines. The flight call is a loud flat yelping *krook* or *klunk,* and the perched call a loud clipped *ga-ga-ga* (or *gro . . .* or *row . . .*). Only the persistent begging note of Carmine nestlings at all closely resembles that of vocally typical bee-eaters.

## *Comfort Activities*

At all stages in the annual cycle the "individual distance" of most bee-eaters is zero. Crowding in the nest, with several adult helpers roosting at night with the parents and the brood, can result in close bodily contact between individuals. Even when bee-eaters roost in the open they commonly pack tightly together and may even "roost in a bunch on each others' backs, three or four deep" (Mackworth-Praed and Grant, 1970). Perhaps that claim is exaggerated but something approaching it can certainly occur.

Toward the end of the breeding season, colonial nests are more like slum tenements, and congestion promotes infestation with a variety of ectoparasites. A majority of 700 Red-throated Bee-eaters examined in the nesting season had substantial swellings on the anterior rim of the cloaca, produced by larval harvest mites (*Neoschogastia* spp., Trombiidae) embedded in the feather papillae. At the same time about five per cent of the population was infected with the mite *Neocheyletiella* sp. (Cheyletidae), causing lesions on the abdominal apterium (Fry, 1969c). Other common ectoparasites of this bee-eater are a hippoboscid fly (*Ornithophila metallica*) and a bird louse (*Meromenopon meropis,* Meroponidae), but none of them seem to be debilitating.

Doubtlessly associated with the prevalence of lousiness is the fact that bee-eaters perform much sun-bathing and dust-bathing (Figure 16). In the commonest sunning posture, bee-eaters perch with the mantle feathers raised, usually but not necessarily with the back to the sun, exposing the skin to its rays. This posture is found in all bee-eaters and its incidence does not bear any obvious relation to weather conditions. A second posture, "broken-neck sunning," is less common. By turning the head to one side and raising the neck feathers, the sides of the neck and chest are exposed to the sun. In a third sunning posture, seen in the European, Carmine, and Large Green Bee-eaters, the birds crouch low with wings and tail outspread and resting on the ground against the hot, sunny slopes at the breeding site.

In most species, dust-bathing is not uncommon, usually occurring in the late afternoon. Bee-eaters usually water-bathe before going to roost, by sweeping low over open water, hitting the surface, and then perching to preen. Short as their legs are, bee-eaters scratch their heads over-wing, or indirectly.

Another behavior, not concerned with grooming but worthy of mention here, occurs from January until March or April when adult Red-throated Bee-eaters in northern Nigeria descend to the ground for a few minutes within 90 minutes of evening roosting time. Shuffling a few centimeters at a time with an awkward walk or hop, a bird selects a small dead leaf, beetle forewing, or piece of grit, and works it in the bill, tossing it up and treating it just as it does its insect food. We do not know that it eats these objects or carries them back to the nest, but before and during the breeding season such bits occur among the debris in the nest chamber. Objects like six-millimeter fragments of stone, pieces of shattered windshield glass, quartz splinters, and fragments of cow teeth and mollusc shells have been recovered from the adult and nestling gizzards, where they probably functioned as gastroliths or pebbles. Perhaps adult birds play with these objects as a vacuum activity. The Australian Rainbow-bird has been credited with placing white bone, mussel shells, and pearl buttons in its nest "for the purpose of illumination" (Sloane, 1916), but another kind of light can now be shed on the habit. In a review of the use of tools by birds, Chisholm (1954) said that "in a reference not now available a Victorian naturalist reported *M. ornatus* . . . holding a small stick in its bill and using it in the fashion of a mining tool" for excavation. The statement needs verifying.

## *Bee-devenoming*

Among Red-throated Bee-eaters reared from the egg in isolation from their species, bee-devenoming behavior or bee-rubbing — beating the insect and rubbing the tip of its abdomen against the perch to induce venom discharge — was elicited the first time honeybees were presented (Fry, 1969a). Obviously, the behavior is innate. Just as obviously, the treatment improves with experience for, not having immobilized the insect adequately, the hand-reared birds were often stung in the mouth and were much distressed. I have never observed symptoms of distress in wild adults, but I have found bee stings embedded in the esophagus of Carmine Bee-eaters as well as in the gizzard walls of Red-throated Bee-eaters and a Black Bee-eater.

While all of the African species have the same devenoming behavior, there is strong circumstantial evidence that the powerful Carmine Bee-eater, which often feeds in continuous flight rather than coming to a perch with each morsel, somehow *devenoms bees while it is flying*: a nice problem. Other bee-eaters return to the perch to immobilize all but the smallest insects. For the remarkably long period of about six weeks, each juvenile Red-throated Bee-eater is closely attended throughout the day by one or two adults, and in the beginning is almost entirely dependent on them for food. Only toward the end of this period do the juveniles make flights after insects and feed themselves for the most part. During these post-fledging weeks the young bee-eater is weaned from non-venomous insects to a diet of venomous ones, and the protracted period of dependence enables the juvenile to perfect the innate but difficult technique of coping with stinging Hymenoptera.

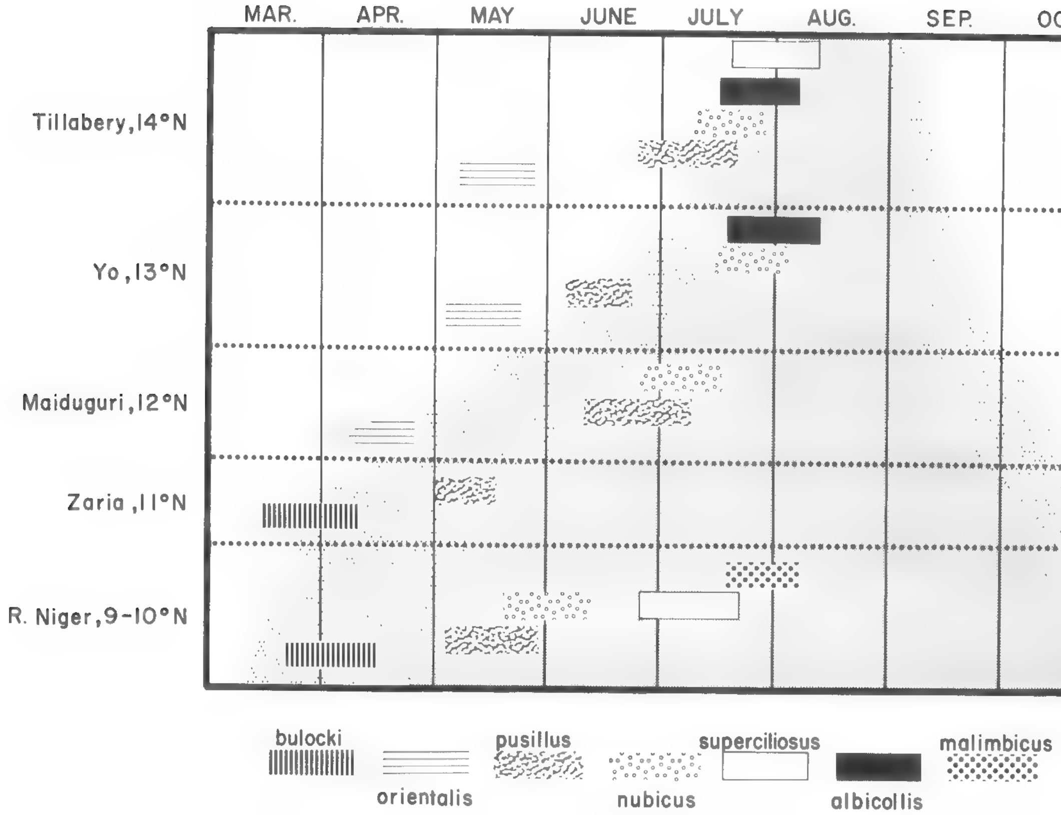


Figure 14. Fledging periods of bee-eaters at West African localities arranged by latitude. Summer rains are shown gray. Periods with an average rainfall of at least 0.6 cm (0.25) per week are pale gray and 2.5 cm (1 inch) per week dark gray. Tillabery (data after Koenig, 1956) is in Niger; the other localities are Nigerian. Fledging periods shown are approximate because of annual variations of about two weeks.

## *Food*

The greater part of the diet of all *Merops* species that I have investigated consists of Hymenoptera, except for Large Green Bee-eaters which specialize on dragonflies and damselflies. Particularly in suburban situations near cities like Salisbury, Rhodesia, and Nairobi, Kenya, diets may comprise honeybees practically to the exclusion of all other insects; but beetles, flies, butterflies, termites, and bugs usually account for substantial parts of bee-eaters' diets, which are nearly always taken in flight.

### Catching Flying Insects

Small bee-eaters, such as the Least, Blue-breasted, Little Green, Boehm's (*M. boehmi,* Figure 17), and Somali (*M. revoilii*) feed by "fly-catching." They keep watch for flying insects from low perches, usually within two meters of the ground — a fence wire or post, a shrub or stout grass stem — and make brief sorties of seldom more than a few meters away, returning to the perch with their victim and immobilizing it there. Like all bee-eaters, they are extremely adept at catching the prey, which seldom escapes.

Middle size *Merops* — Swallow-tails, Cinnamon-chesteds, Red-throats, White-fronts, White-throats, and Black Bee-eaters — also behave like flycatchers, returning to the perch to beat their prey. But they select more elevated vantage points, fly farther after insects, and range more widely, foraging during the course of a day over hundreds of acres or along as much as a mile of wooded watercourses. Upon alighting, these species swallow small insects, for example the 5-mm-long, stingless "sweat-bees" (*Trigona* spp.), without treatment, but they immobilize larger insects before eating them. Among Red-throated Bee-eaters, the mean of 66 counts of feeding flights, made in and out of the breeding season in all weather, was 5.2 sorties every 10 minutes. Since these birds average 11 waking hours a day in active feeding and make very few sortie flights without capturing an insect, an individual Red-throated Bee-eater must eat about 340 insects a day or 124,000 insects a year.

Large birds such as the Large Green, Rosy, European, and Carmine Bee-eaters tend to use treetop perches and to range even more widely, over a few square miles daily. They are also more prone to hunt in continuous flight. I have seen European Bee-eaters twisting and wheeling in flight high over the savannas, catching probably soft-bodied insects such as flying ants and termites. With a large and hard-bodied insect, they must return to a perch to immobilize it by beating and devenoming it before eating it.

Carmine Bee-eaters (Figure 18), as I mentioned earlier, may devenom bees on the wing; I have netted them with bills sticky with the characteristically smelling venom of *Apis* under circumstances strongly suggesting the bees had just been caught aloft. The Carmine is of particular interest in two other respects: First, having a predilection for grasshoppers it is among the first birds to arrive at a bush fire — along with Black Kites (*Milvus migrans*) and Grasshopper-buzzards (*Butastur rufipennis*) — to prey on fleeing grasshoppers and other insects. Second, Carmine Bee-eaters of the northern savanna population (*M. nubicus nubicus*) habitually perch on large animals, preying on the insects they disturb (Figure 19). They ride on goats, cattle, antelopes, ostriches, bustards, and even storks and, judging from the frequency of the sorties of bee-eaters accompanying cattle grazing the savannas, the animals must provide an excellent source of food. Strangely, there are no records of southern Carmine Bee-eaters (*M. n. nubicoides*) using animate perches.

## Non-flying Arthropods

Red-throated Bee-eaters, kept in roomy outdoor aviaries, very seldom took perfectly suitable insect food from the ground, not even bees crawling

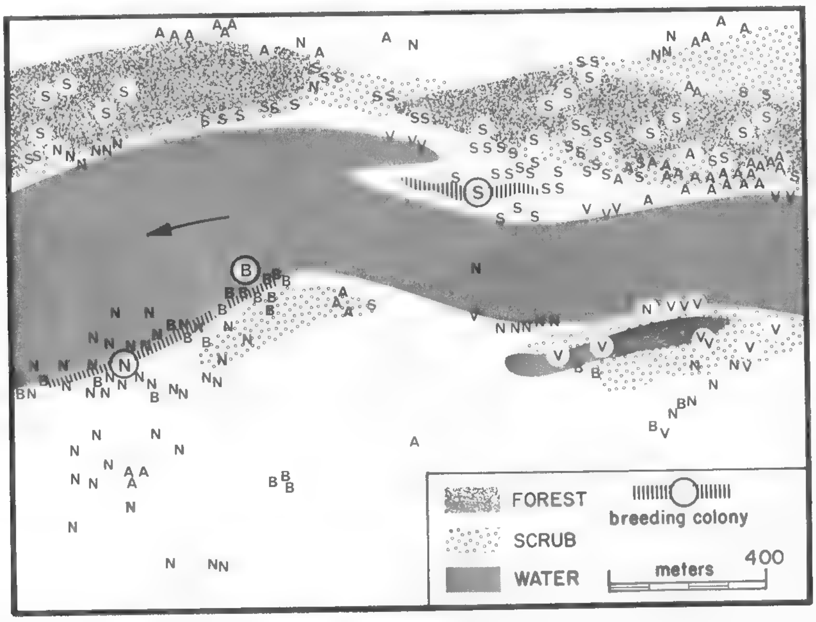


Figure 15. Feeding stations of five bee-eater species on the River Niger (8° 45′ N) on 14 May. V = Least Bee-eater, with several nests in the river banks; S = Rosy Bee-eater, a colony of about 25,000 located on the sand spit; N = Carmine Bee-eater, a colony of 1,000; B = Red-throated Bee-eater, a recently-fledged colony of 100; and A = White-throated Bee-eater, about 100 birds on passage. Most Rosy and Carmine Bee-eaters dispersed well away from this area to feed.

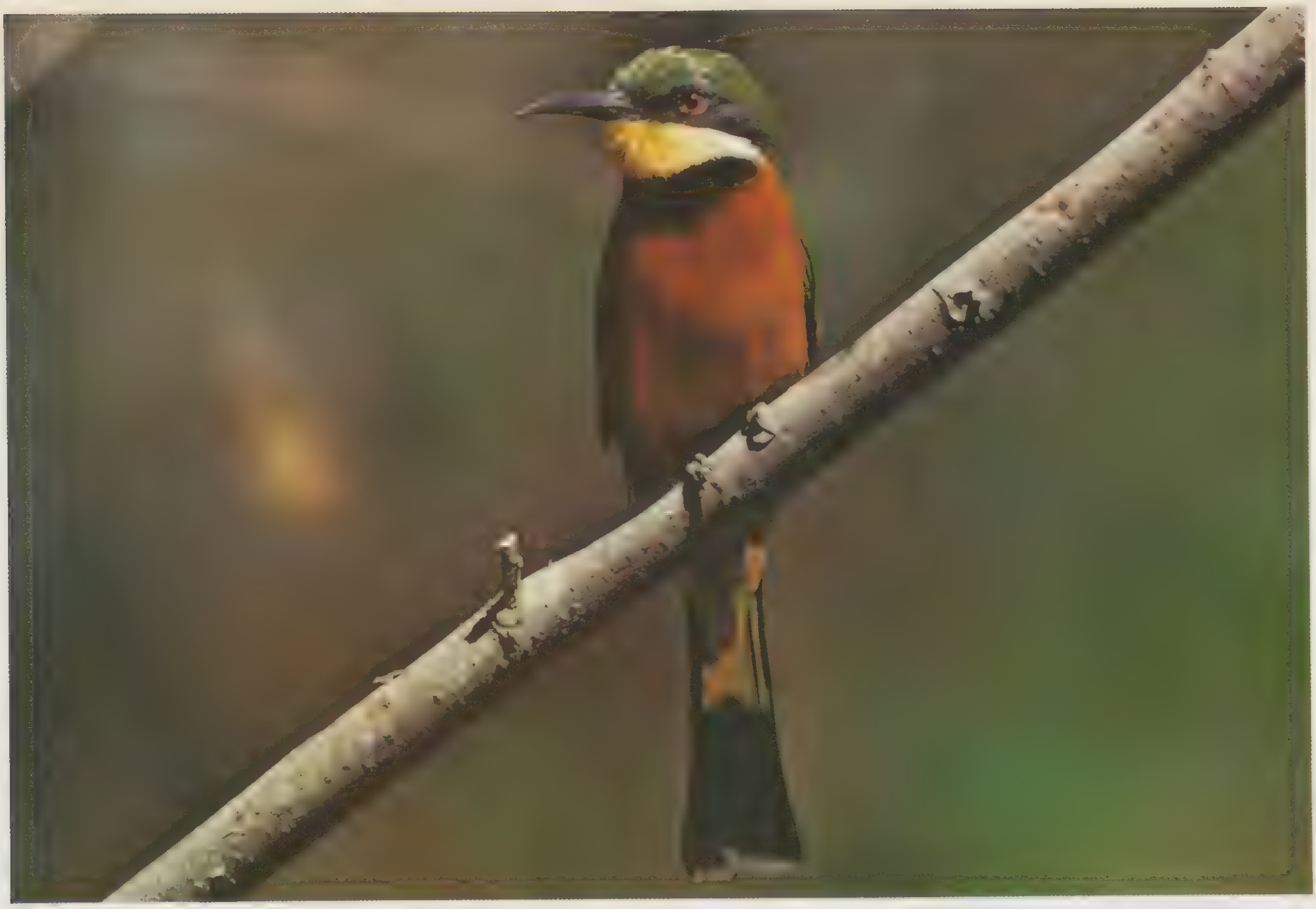
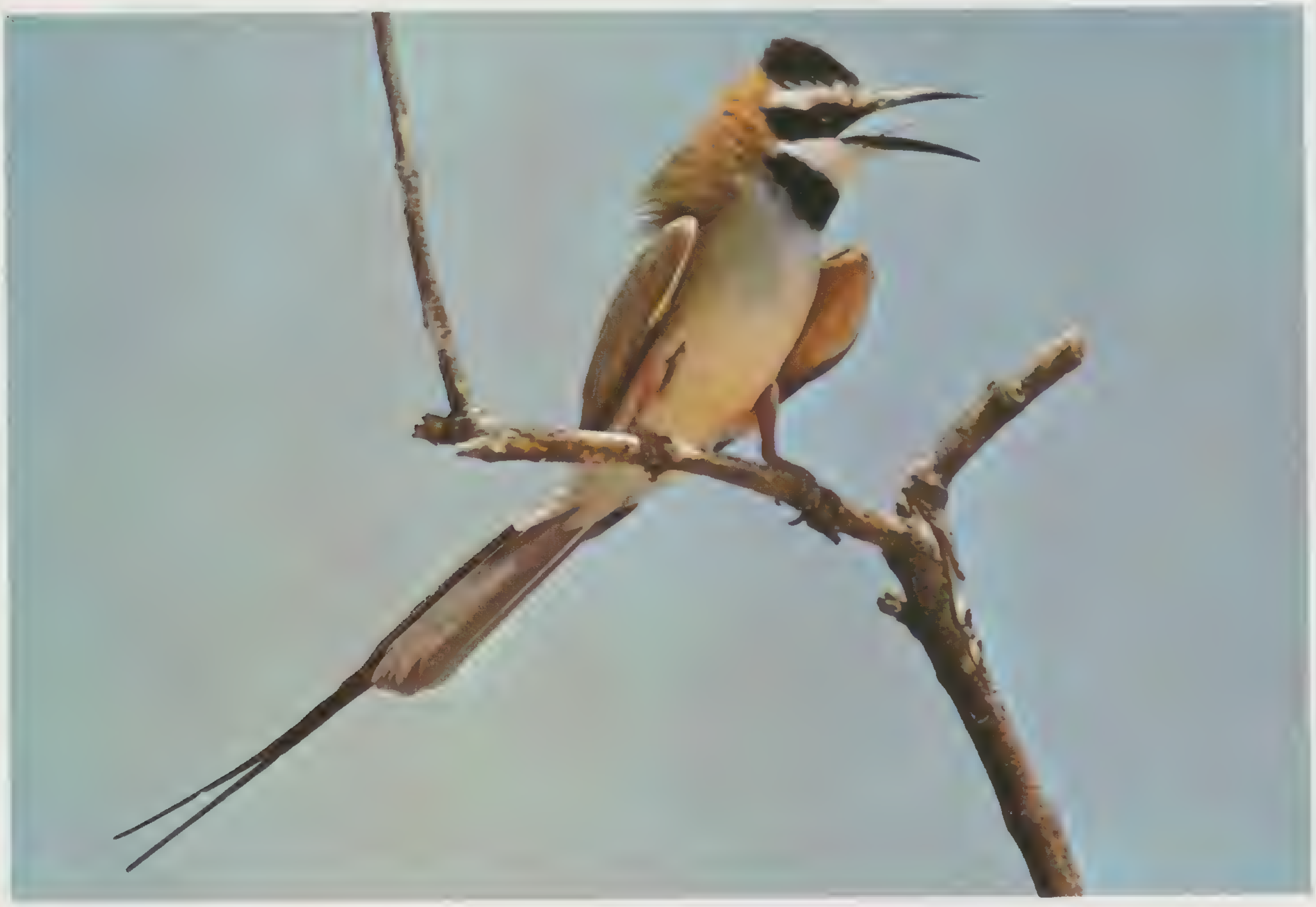


Plate II. *Above,* Cinnamon-chested Bee-eater, *Merops oreobates.*
*Below,* White-throated Bee-eater, *Merops albicollis.*



over the perch a few inches from them. However, aviculturists have successfully kept several other bee-eater species on a diet of fresh and frozen insects which the birds took from feeding trays. Callegari (1956, 1970) fed his bee-eaters a mixture of 60 per cent mealworms, 20 per cent honeybees, and 20 per cent other insects, and also induced them to take freshwater shrimps and lettuce.

The only non-flying insects that I recorded in the diets of wild bee-eaters were soldier driver-ants (*Dorylus* sp.) and myrmeleontid (Neuroptera) and noctuid (Lepidoptera) larvae in White-throated Bee-eaters at Lake Chad, and many lepidopteran caterpillars up to seven millimeters long in European Bee-eaters in Rhodesia. The last two birds have somewhat atypical diets as discussed below.

Osmolovskaja and Formosov (1955) recorded harvestmen (Opiliones) and spiders in the gizzards of European Bee-eaters from the lower Volga.

From time to time we have reports of aberrant feeding. Little Green and Swallow-tailed Bee-eaters pick insects off flowers and leaves, according to Mackworth-Praed and Grant (1970), and European Bee-eaters dive into water apparently after small insects floating at the surface (Foenander, 1956) or below it (Barham *et al.,* 1956; Sage, 1960; Tree, 1960). There are reports of similar behavior in Large Green Bee-eaters (Sage, 1960) although some records for this bird and for Little Greens may refer to bathing, not feeding (White, 1960; Took, 1963).

## Other Foods

Large Green Bee-eaters, which seem to be more wedded to watercourses and waterside habitats than most other bee-eaters, have been recorded diving into water not only for insects but also for small fish.

In northeastern Nigeria, at the place where nests of the White-throated Bee-eaters were discovered for the first time in 1965, I saw this species carrying to the nest lizards about four centimeters long, probably *Mabuya* sp. (Scincidae).

Twenty-five European Bee-eaters, found dead after an exceptionally cold spell in Rhodesia in November 1968, had a mean weight at least 15 per cent less than normal, and five of them had the hard berries of *Cedrella tuna* stuck in their throats (Steyn and Brooke, 1970).

The most remarkable instance of an unusual food for a bee-eater is recorded for the White-throated. Studying this species on its "wintering" grounds in southern Nigeria, I found, in the gizzards of six out of 25 birds, strips up to 16 mm long of the fibrous, oily red epicarp of the oil palm (*Elaeis guineensis*) fruit. It is extremely nutritious and rich in lipids and is eagerly sought after by a variety of birds and mammals, including such an unlikely carnivore as the Grey Kestrel, *Falco ardosiaceus* (Wells, 1965), and is the staple food of the Palm-nut Hawk (*Gypohierax angolensis*). How the bird obtained the strips of fruit defied my imagination. At the time, I wrote "although this bee-eater does descend to the ground for food more readily than other species, the epicarp could well have been stripped from the fruits *in situ* rather than from the fallen fruits." The real explanation was far more remarkable. Pettet (1969) found redless striped squirrels (*Funisciurus anerythrus*) feeding on the fruits hidden in the dense crowns of the palms by holding one at both ends and tearing off strips of the epicarp to get at the more succulent mesocarp. Up to 10 White-throated Bee-eaters gathered around the

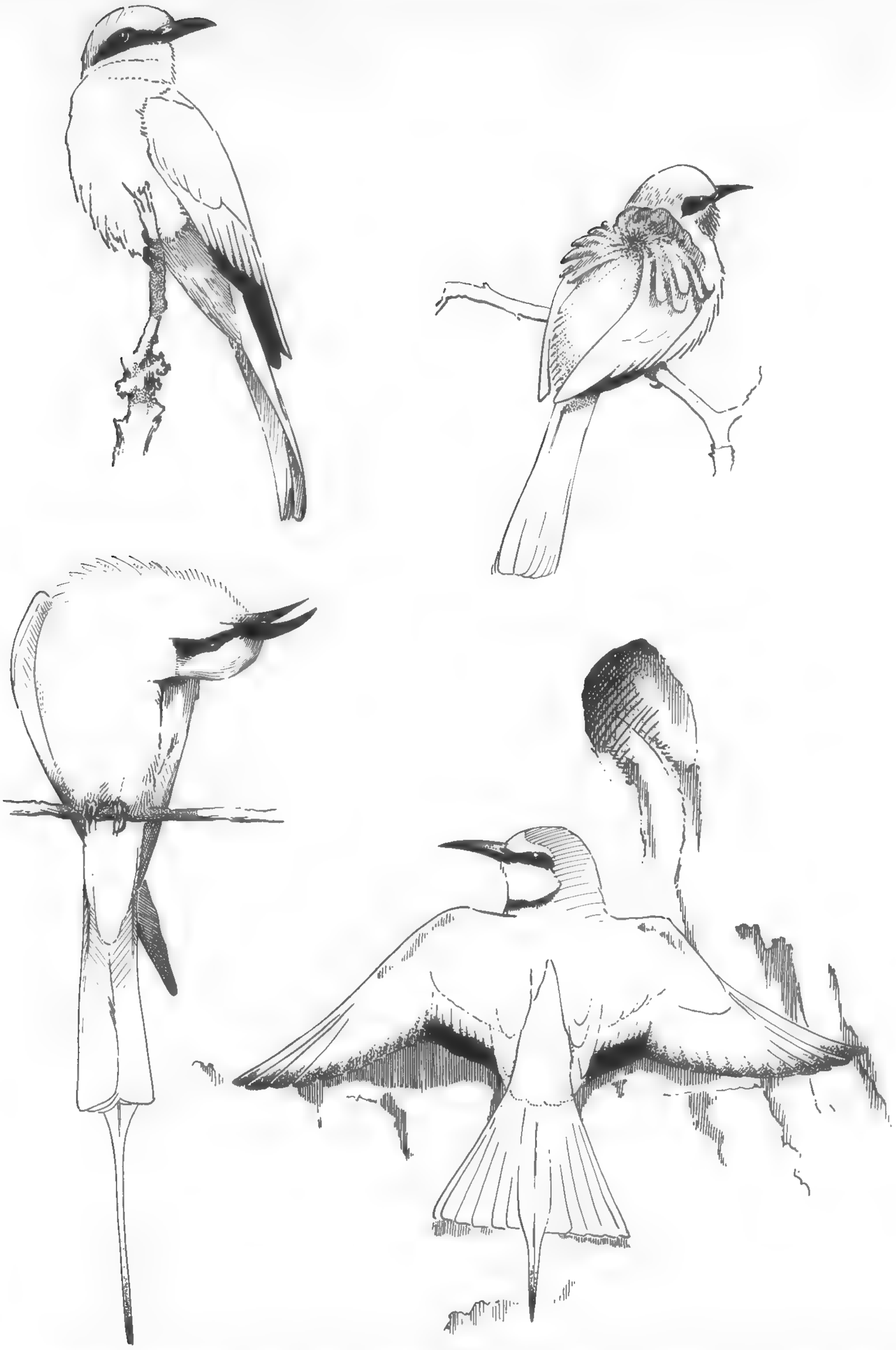


Figure 16. Comfort postures. Top left, resting (White-fronted Bee-eater). Top right, sunning with raised mantle (Red-throated Bee-eater). Bottom left, "broken-neck" sunning (Carmine Bee-eater). Bottom right, sunning on cliff slope (European Bee-eater, below its nest entrance).

palm, even perched on the fronds within a foot of the squirrels, intercepting with great efficiency the strips as they fell just below frond-level.

Pettet thought that the bee-eaters probably use this source of food whenever the opportunity arises, and so there may not be the connection that I formerly postulated between this lipid-rich diet and the birds' fattening before the spring migration from the forest zone to the southern edge of the Sahara Desert (Fry, 1967b).

## Analytical Method

I studied the diets of bee-eaters by analyzing the contents of gizzards and regurgitated pellets that litter the ground copiously beneath perches and form

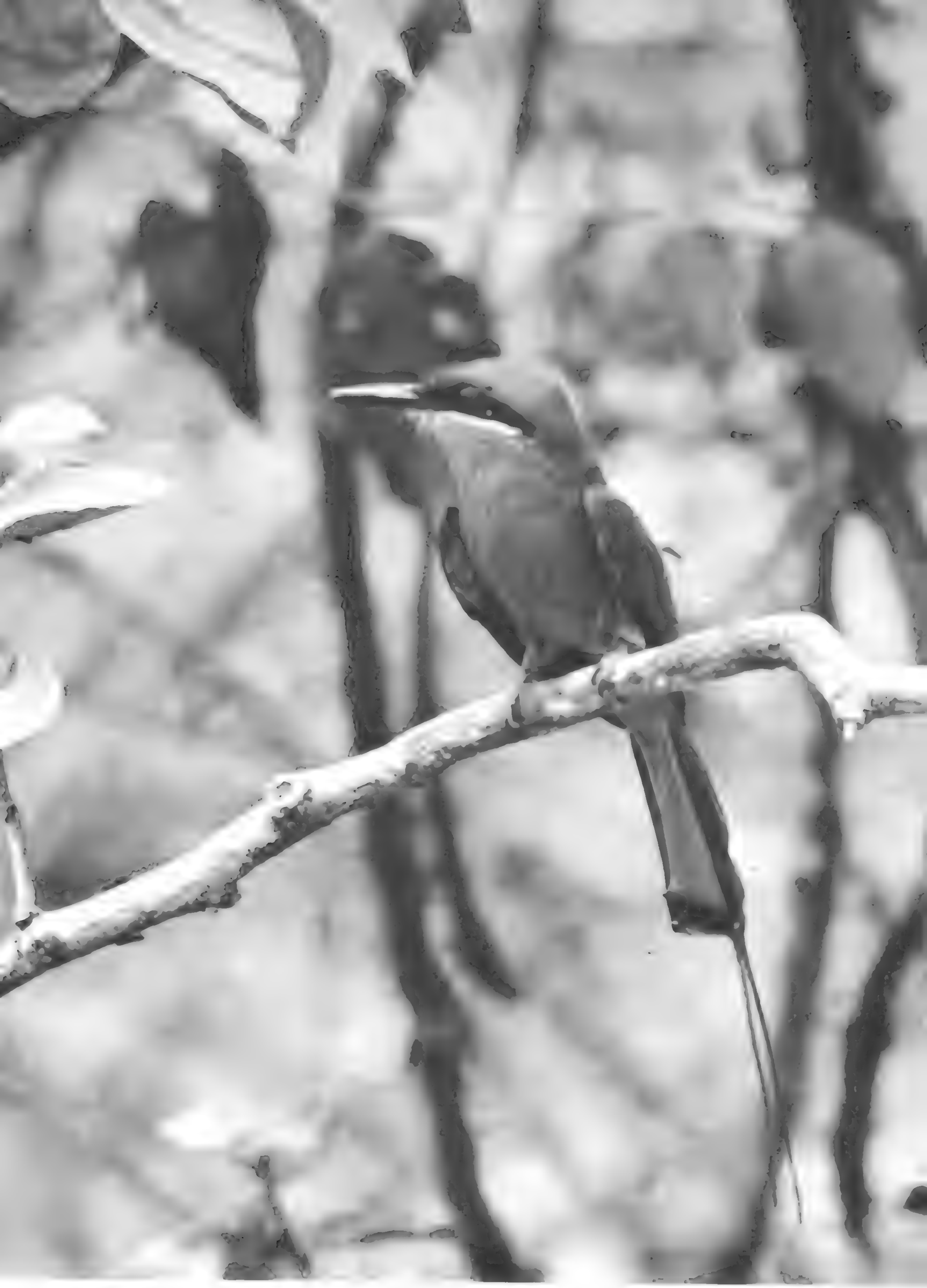


Figure 17. An adult Boehm's Bee-eater photographed near its nest in the Lengwe Reserve, Malawi.

a thick debris in the nests. One must be careful to ensure that the pellets, collected at one site, are from only one species of bee-eater. I generally collected a sample of 10 fresh-looking, unbroken pellets at a time, destroying any remaining under the perch so that I would find only freshly cast ones the next time.

I teased each sample in 70 per cent alcohol, examined each pellet under a variable-power binocular microscope, and sorted out head capsules, mandibles, elytra, wings, and other recognizable fragments for identification (Figure 20). Each Red-throated Bee-eater pellet contains remains of 18 insects on the average, and I have identified over 4,000 insects from this species and 12,000 from 13 other African *Merops* species. Hartley (1948) remarked that the pellets cast by Large Green Bee-eaters show no remnants of the pierid butterflies he had observed the birds eating, and he recommended that one should never use pellet analysis alone in the assessment of the food of birds. In the present study, evidence indicates that all chitinous parts of ingested insects are cast up in bee-eater pellets. Some, like Lepidoptera, being softer and more translucent, are more easily damaged and more readily overlooked during microscopic sorting than others. But I easily recognized termite heads, 0.7 mm in diameter, and found that bee-eater pellet analysis produces qualitatively accurate results that are also acceptably accurate quantitatively.

## Diet of Adult Red-throated Bee-eater

I collected pellet samples throughout the year at Zaria. Easily the most important single item of food is the honeybee, which comprised, on the aver-

Figure 18. Adult Carmine Bee-eater sitting near its nest in a colony in Rhodesia.

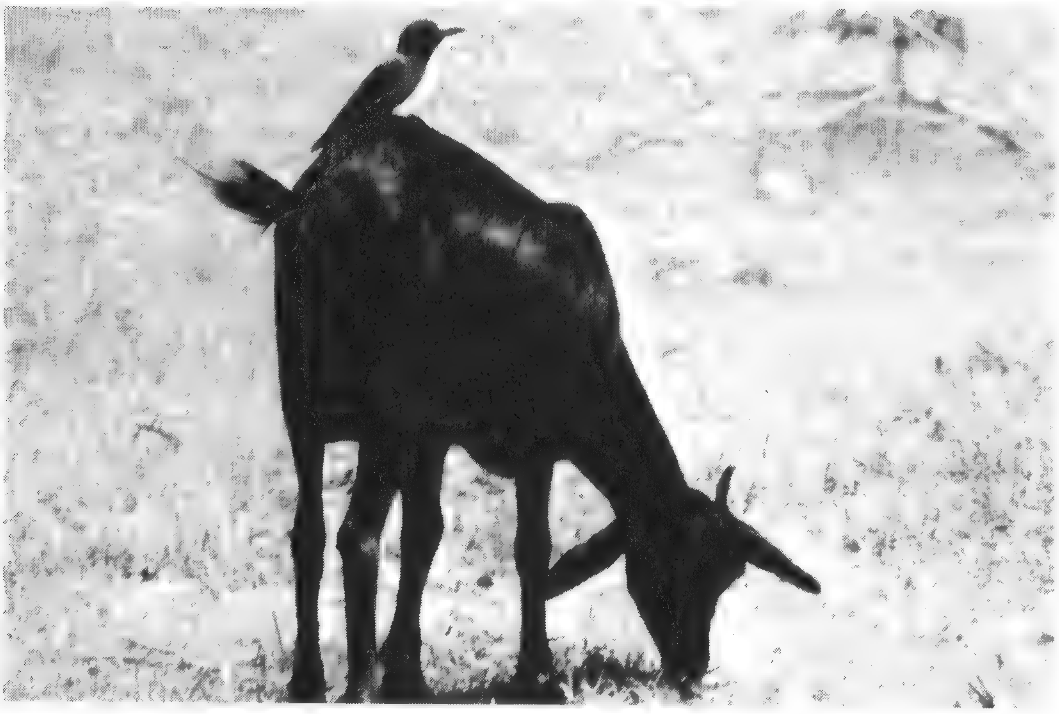


Figure 19. Northern Carmine Bee-eaters often hunt from animal perches.

age, 25 per cent of the food items taken, varying from less than 5 per cent in July and August to more than 45 per cent in March, April, and June. The proportion of honeybees in the diet by weight or volume would be much greater, since at 55 milligrams it is one of the largest insects eaten. As with other bee-eaters, the great majority of the bees were workers — venomous females — and only seven out of 956 bees were drones — non-venomous males. Some birds can discriminate between drones and workers of honeybees (Lacey, 1910, for the Swift *Apus apus;* Grant, 1945, for the tyrant flycatchers *Tyrannus* and cliff swallows *Petrochelidon).* Red-throated Bee-eaters (Fry, 1969a) and, in Czechoslovakia, European Bee-eaters (Matousek, 1951) recognize and select drones; but I would not expect that a bird that lives on venomous workers should prefer drones. In Red-throated Bee-eaters, the disparity between drones and workers reflects the relative abundance of the castes in the field; in aviary studies there was no evidence of a preference or selection between drones and workers (Fry, 1969a).

Of the 3,886 insects examined from the pellets of adult Red-throated Bee-eaters, about four species of the small stingless bees *Trigona* made up 16 per cent; and all Hymenoptera comprised 79 per cent. Of the remaining food, flying beetles made up 14 per cent; Odonata, Orthoptera, termites, moths, and butterflies, less than 2 per cent; bugs and flies, 5 per cent. At least 175 species of Hymenoptera and 90 species of other insects were represented.

Seasonal variations in diet correspond broadly with what little is known about the seasonal abundance of diurnal flying insects at Zaria (Figure 21). Peaks of the following insect groups represented in the diet of adult Red-throated Bee-eaters correspond with seasonal peaks of the groups in nature: Cicadidae, Calyptratae, *Apterogyna* (Apterogynidae), winged ants, *Halictus* (Halictidae), *Trigona, Anthophora,* and *Ceratina* (Apidae), and buprestid beetles.

I did not determine whether the dietary ratio of four hymenopterans to one other insect reflected the relative abundance of these groups in the field, and I cannot say whether the bee-eaters eat more Hymenoptera because they

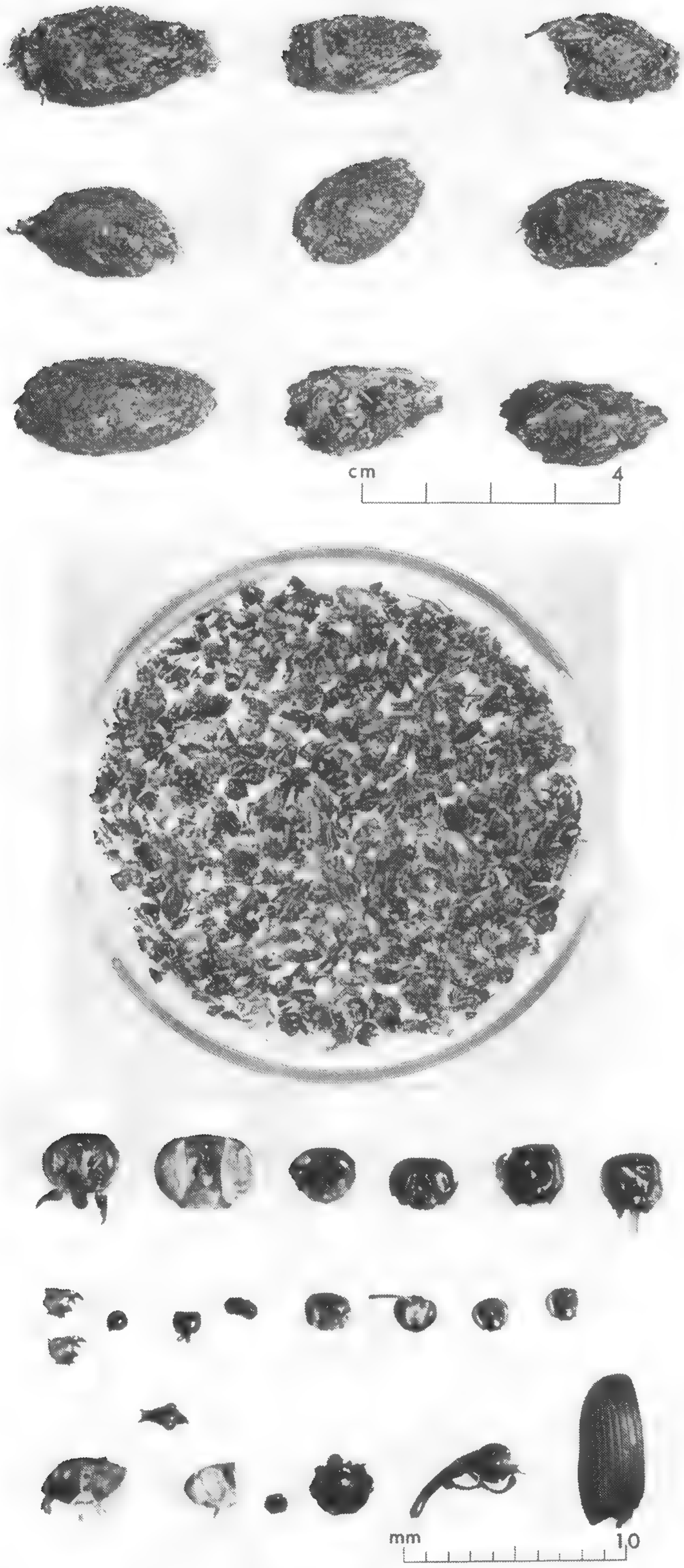


Figure 20. Top: pellets of Large Green Bee-eater (left), White-fronted Bee-eater (center), and European Bee-eater (right). Middle: one pellet disintegrated. Bottom: identifiable sclerites from one pellet, including odonate mandibles, heads of three beetles, two flies, a bug, two worker honeybees (upper row, right), and 11 other Hymenoptera.

prefer them or because they are more common. The only suitably sized flying insects that the Red-throats ignored were some acraeid and most pierid butterflies and some danaids like the African monarch (*Danaus alcippe*). Captive bee-eaters also rejected these butterflies, which are warningly colored and probably distasteful.

### Diets of the Nestling and Fledgling Bee-eaters

In the field, I noticed that food taken to nestling Red-throated Bee-eaters consisted not of the usual adult diet of Hymenoptera up to the size of honeybees, but rather of a variety of larger insects like dragonflies, butterflies, and moths (Sphingidae, Pieridae, Satyridae, Nymphalidae), Orthoptera (crickets and long- and short-horned grasshoppers), as well as some large Hymenoptera. The gizzards of four nestlings contained 17 cicadas (*Platypleura truncaticeps*) and six large lepidopterans, but only two wasps, three *Trigona* bees, and three small beetles. Only six cicadas, all the same species, were ever found in gizzards or pellets of adults, and I infer from this and other observations that Red-throats carry to the nest only non-venomous insects and larger items of prey. Perhaps economy of effort is involved here.

Among pellets cast by young bee-eaters within four weeks of fledging, only 3 per cent of over 300 insects were honeybees — a proportion much lower than in adults at the same time. This post-fledging period of about six weeks sees the gradual weaning from the nestling diet of large non-venomous insects to the adult diet of 25 per cent stinging honeybees.

### Bee-eaters with Similar Diets

Many other savanna bee-eaters in Africa prey upon the same insects as Red-throats, taking them in similar proportions. Because it groups higher taxonomic categories and does not show individual prey species except honeybees, Figure 22 exaggerates dietary differences. I shall emphasize the real resemblances in bee-eaters' diets, at the level of individual prey species, by statistical treatment in a forthcoming paper. Suffice it to say here that besides similarities in the gross proportions of higher taxa of insects consumed by several of the bee-eaters, species after species of insects recur in pellets of nearly all the bee-eaters examined. Hymenopteran examples are: *Oneilella, Peltochalcidia, Epyris, Campsomeris, Elis, Mutilla, Camponotus, Cryptocheilus, Pseudagenia, Eumenes, Polistes, Ropalidia, Odontodynerus, Liris, Piagetia, Tachysphex, Sphex, Sceliphron, Philanthus, Cerceris, Halictus, Nomia, Megachile, Anthophora, Ceratina, Trigona* and, of course *Apis* (honeybees). So similar are the diets that qualitative data, or the different kinds of insects in the diet, could not be used to identify the specific bee-eater predator; quantitative data, or the proportions of the different insects in the diet, might give a clue but only for the bee-eaters discussed in the next section.

There is a broad correlation between the sizes of bee-eaters and the sizes of their prey. This is more apparent if flying ants and termites, the small insects for which all bee-eaters have a predilection (see Rand, 1936, for Large Green Bee-eaters), are discounted (Fry, in prep.). Only the small bee-eaters prey to any extent on flies — 5 per cent in the Blue-breasted, 6 per cent in the Least, and 17 per cent in Boehm's Bee-eater. A fruitfly (*Drosophila*) from a Least Bee-eater is the smallest insect I have found in any bee-eater.

Another reason for the apparent differences in specific diets (Figure 22) is the high proportions of honeybees in the pellets collected at certain localities. Most of the material of the Cinnamon-chested, Swallow-tailed, White-fronted, and Carmine Bee-eaters is from the vicinity of Nairobi and Salisbury. Clearly honeybees are abundant there; the pellets of the same bird species from some other parts of Africa have much lower proportions of them. The White-fronted Bee-eater in Rhodesia eats twice as many honeybees as its close relative, the Red-throated Bee-eater, in Nigeria; otherwise, their diets are almost identical in composition.

Other studies, employing various methods of investigation, showed that the Rainbow-birds in Australia eat much the same kinds of insects, in similar proportions (Serventy and Whittell, 1962), as do Bay-headed Bee-eaters in Malaysia (Pagden, 1958), Large Greens in Niger Republic (Koenig, 1953), Blue-headed and Swallow-tails in Ivory Coast (Thiollay, 1971), Cinnamon-breasteds in Kenya (van Someren, 1956), and European Bee-eaters in Belgium (Bastien, 1957), Denmark (Larsen, 1949), and France (Swift, 1959).

## Some Divergent Diets

*Large Green Bee-eater.* — I have examined 800 insects from pellet samples collected at 10° N Lat. on the Niger at Lake Chad in République Centrafri-

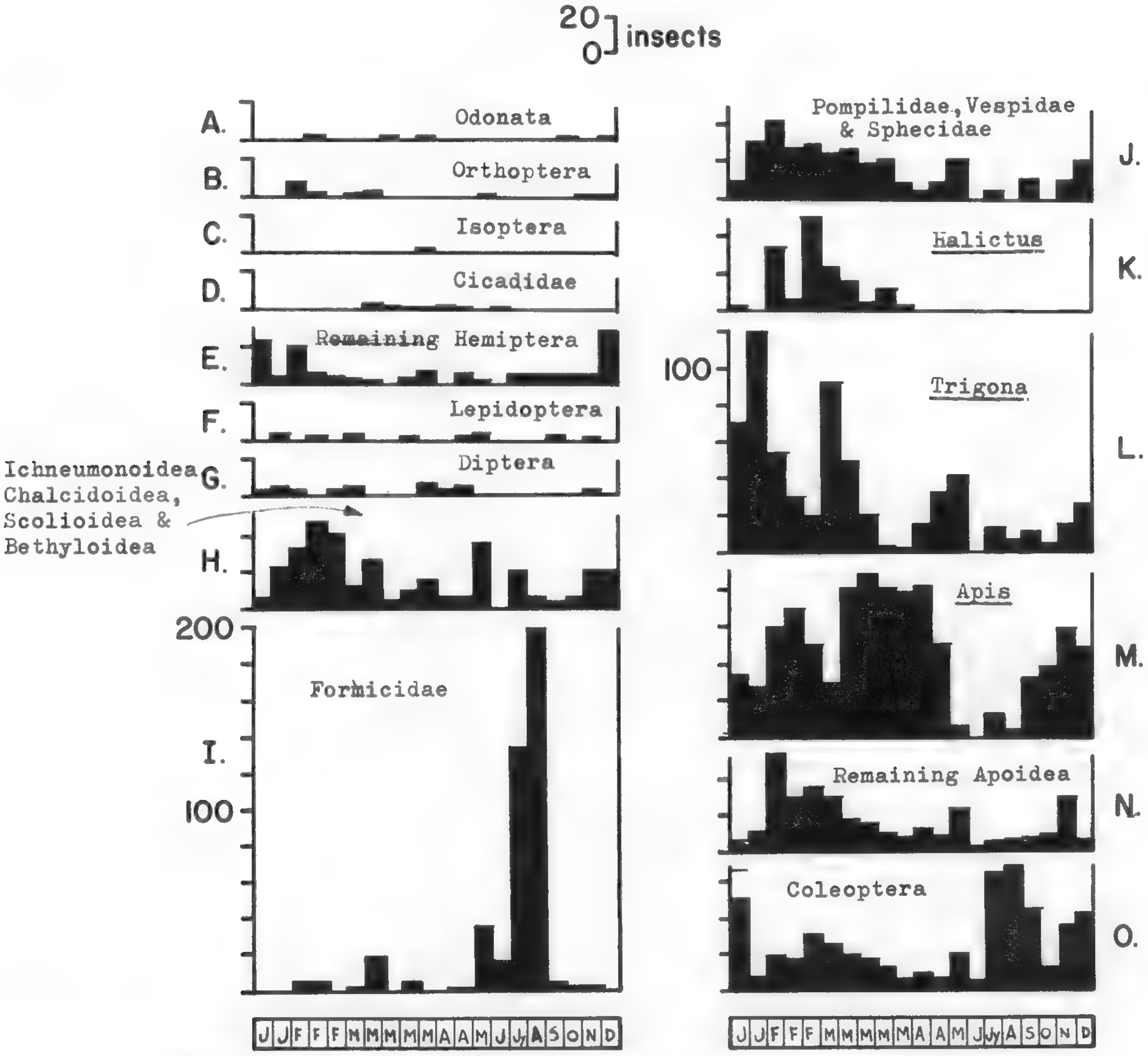


Figure 21. Seasonal distribution of components of the diet of adult Red-throated Bee-eaters at Zaria, Nigeria. More pellet samples were collected over the breeding season, January to April, than during the rest of the year. The letters signify the following groups of insects: A, Odonata; B, Orthoptera; C, Isoptera; D, Cicadidae; E, other Hemiptera; F, Lepidoptera; G, Diptera; H, Ichneumonoidea, Chalcidoidea, Scolioidea, and Bethyloidea; I, Formididae; J, Pompilidae, Vespidae, and Sphecidae; K, *Halictus;* L, *Trigona;* M, *Apis;* N, remaining Apoidea; O, Coleoptera.

cain, as well as a few from the closely allied Blue-tailed Bee-eaters in Malaysia. Everywhere I found a high proportion of Odonata, an average of 67 per cent. Though neither the Central African nor the Malaysian material was from particularly watery habitats, I believe that these birds are specialists on dragonflies and damselflies. At the same time, honeybees comprise 10 per cent of the diet, the remainder being other Hymenoptera, beetles, bugs, and butterflies.

*Carmine Bee-eater.* — In the inundation zone of the Niger (Remaudière, 1954) and in the Congo (Chapin, 1939), Carmine Bee-eaters feed largely on big acridid grasshoppers; and Davey (1955) and Nickerson (1958) indicated that the migration of locusts, particularly *Locusta migratoria,* may determine the seasonal movements of this bird. They also eat *Schistocercus* and *Ornithacris.* My analysis of nearly 2,400 insects in pellets from several Nigerian and Rhodesian localities shows that acridid grasshoppers do not form a major part of the diet of this bee-eater over the whole of its range. Numerically, they constituted only 3.4 per cent of the adult diet and 8 per cent of the nestling diet; but these figures were depressed by great numbers of flying ants in several samples, and the Orthoptera fraction of the adult diet by weight would probably be in the order of 50 per cent.

The nestlings' diet, in a colony on the Ngadda River in northeastern Nigeria, was largely an 18-mm-long bug (*Coridius viduatus,* Pentatomidae). Nestlings in a colony on the Umfuli River in Rhodesia received one species of chafer (Scarabeidae) almost to the exclusion of other insects. This suggests that Carmine Bee-eaters, like many birds, are to an extent opportunists, taking that food which they can capture the most easily.

*White-throated Bee-eater.* — This is the only bee-eater that regularly eats vegetable matter, and it is also unusual among African bee-eaters in that it frequently takes food from the ground — small lizards, flightless beetles, ants, larvae, and so on — at least in "Sahel" savanna. While over 90 species of hymenopterans and nearly 90 of other insects are represented among the 2,500 individual insects examined from pellets, much the largest fraction, 56 per cent, of the adults' diet consists of flying ants.

Ants are scarce in the diet fed to the nestlings, but acridid grasshoppers and moths are abundant. Orthoptera form 50 per cent of the nestlings' diet and only one per cent of the adults'. Other notable items of nestling food include the 70-mm-long ant-lion (*Palpares,* a neuropteran of the family Myrmeleontidae), the 22-mm-long carpenter-bee (*Xylocopa,* which weighs about 1.0 gm), and the 36-mm-long sphecid wasp (*Chlorion xanthocercus*).

*European Bee-eater.* — While the European Bee-eater preys on honeybees to such an extent that attempts in the past have frequently been made to control the species as a pest (Kraft and Korelov, 1938), it does seem to have a rather generalized and opportunistic diet of flying insects. Pitman (1929) found that in migrants in Kenya and Malawi, Orthoptera (including *Locusta*) comprised over 50 per cent of the food. Swift (1959) reviewed the work of 12 authors in Europe, reducing diverse means of analysis to a simple notation, from which we can infer that the diet is 25 per cent Odonata, 2 per cent Orthoptera, 12 per cent Lepidoptera, 4 per cent Diptera, 36 per cent Hymenoptera, and 21 per cent Coleoptera. He found that beetles and hymenopterans predominate in May, beetles and dragonflies in June, and dragonflies and butterflies in July. I identified 850 insects in 60 pellets from Rhodesia and found 85 per cent of the diet there to be composed in almost equal proportions of ants,

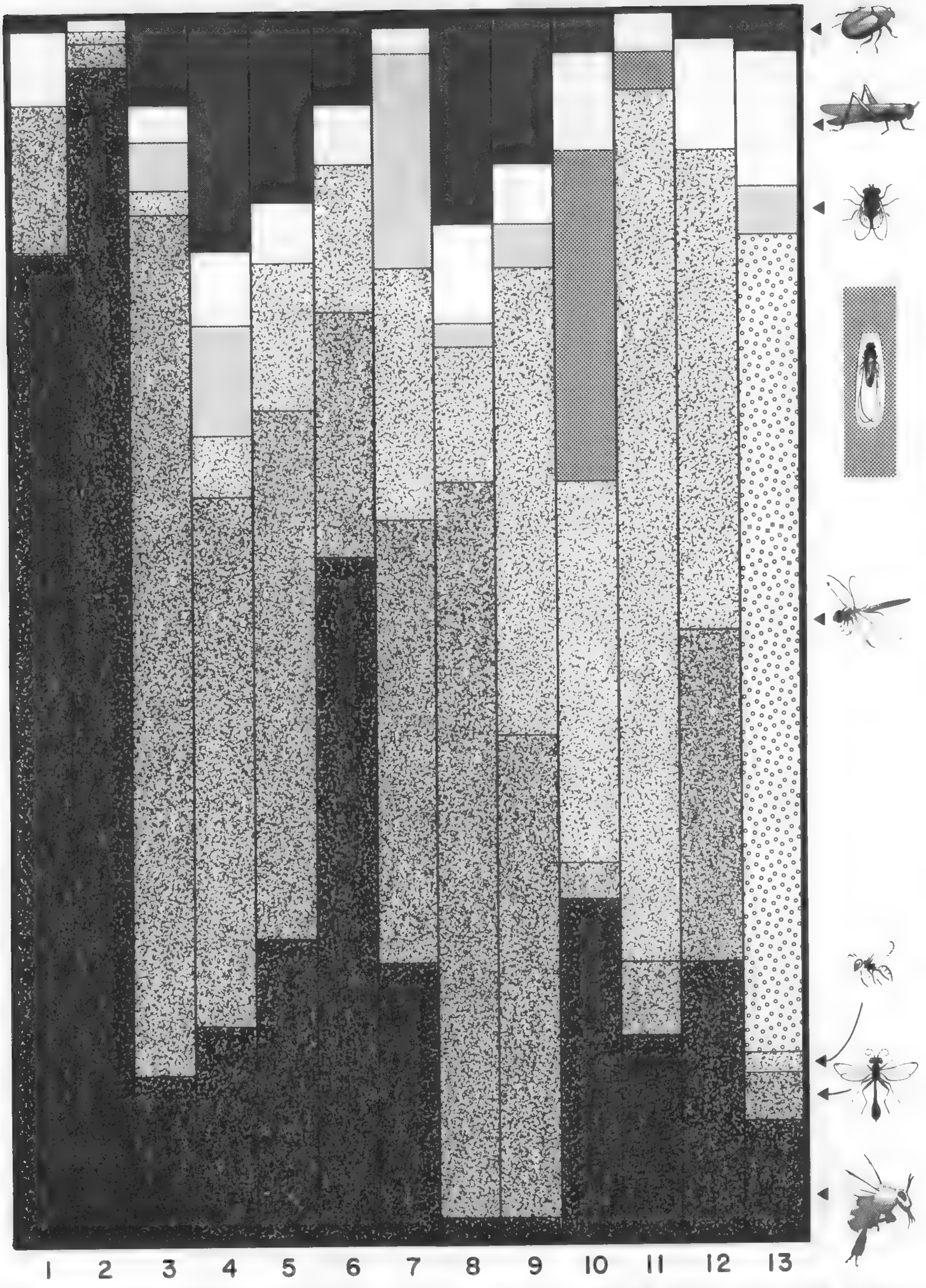


Figure 22. Proportions of constituents in the diets of 13 species of *Merops* in Africa. Symbols and shadings represent (from top to bottom): beetles; grasshoppers and other items; flies; termites; dragonflies and demoiselle-flies; ants; Hymenoptera except ants and honeybees; and honeybees. "Other items" are mainly bugs, moths, and butterflies, but also see text. Note that the proportions shown are based on numbers of diet items, not volume or weight. Numbers at the bottom indicate the following species and the sample size or number of food items (in parentheses): 1, *hirundineus* (315); 2, *oreobates* (787); 3, *variegatus* (235); 4, *pusillus* (1,022); 5, *bulocki* (3,886); 6, *bullockoides* (1,122); 7, *boehmi* (289); 8, *orientalis* (383); 9, *albicollis* (2,468); 10, *apiaster* (860); 11, *malimbicus* (1,240); 12, *nubicus* (2,364); 13, *superciliosus* (794).

termites, and honeybees; the remainder consisted of the same insects as occur in other bee-eaters' diets.

## *Discussion*

### The Bee-eating Niche

By far the most important single constituent of bee-eaters' diets, at least in Africa, is the honeybee. It has a very wide natural and semi-cultivated distribution over the whole of sub-Saharan Africa and, indeed, is now virtually cosmopolitan. Where honeybees are common, bee-eaters consume them almost to the exclusion of other foods. Bee-eaters have been considered pests when flocks persist in feeding at apiaries.

At Zaria, C. Jessen (pers. commun.) reported that the only other predator of honeybees at his hives was the abundant agamid lizard (*Agama agama*), but we know that several birds consume them under other circumstances. Grant (1945) listed 40 North American birds from nine orders known to eat honeybees occasionally, and they may even be a regular feature in the diet of such thin-billed birds as the Black Wheatear (*Oenanthe leucura*) according to Richardson (1965).

In Africa, the ratel or honey-badger (*Mellivora capensis*) and the wintering Honey-buzzard (*Pernis apivorus*), both scarce, subsist largely on the contents of honeybees' nests — wax, honey, larvae, and adult bees; and honeyguides feed on larvae if not on adult insects, too. Other Hymenoptera feature regularly in bird diets; an economic study in Russia found that 10 passerine species, out of 16 samples, had eaten aculeate Hymenoptera (Charlemagne, 1954). For the most part, however, it appears that bee-eaters encounter little direct competition for Hymenoptera and that they occupy the niche of predation on larger, venomous, flying Hymenoptera practically alone.

In the Neotropics, the jacamars (Piciformes, Galbulidae) occupy exactly the same niche, and exhibit an astonishing degree of convergence with the bee-eaters in respect to plumage, bill and leg conformation, and breeding biology. These and other resemblances stem from the fact that their diets are so similar (Fry, 1970a, 1970b). It suggests that venomous-bee-eating is a specialized niche, an adaptation that has largely determined the evolution of jacamars and bee-eaters.

### Ecological Isolation in *Merops*

With the exceptions of diets and outlines of the biology of European and Red-throated Bee-eaters, our knowledge of the Meropidae is still fragmentary and superficial. I have presented above the information available in such a way as to emphasize the differences between species. The two Asiatic species of *Nyctyornis* are certainly different enough from other bee-eaters to warrant generic separation. The Celebes Bee-eater (*Meropogon forsteni*) has a unique mosaic of morphological distinctions, but we know nothing of its biology. In the Congo, the heavy bill of the equally mysterious Black-headed Bee-eater (*Merops* [*Bombylonax*] *breweri*) suggests ecological differentiation with respect to most bee-eaters. The remaining 20 species of *Merops* show uncommon uniformity in habits as well as structure. It is the more remarkable when we consider their wide range and antiquity in the Old World — the Australian Rainbow-bird arrived in Australia not later than the early Pleistocene or even late Pliocene (D. L. Serventy, pers. commun.) — and their degree of sympatry, or overlapping ranges.

Broadly speaking, most African species of *Merops* have different habitats: the Somali, Large Green, Little Green, and White-throated Bee-eaters breed in sub-desert steppe; the Boehm's, Red-throated, White-fronted, Swallow-tailed, Cinnamon-chested, and Carmine Bee-eaters inhabit woodland; the Least and Blue-breasted live in grassland and swamps; the Black and Blue-headed occur in forest and the Rosy feeds above it. All of these, however, are partial to waterside situations, partly because they provide cliffs suitable for nests. Individuals and flocks range freely into neighboring habitats; and most species are migratory, some having quite different winter habitats — for example, the White-throated, Large Green, and Rosy Bee-eaters. Thus, as many as five species commonly occur together, in separate flocks, but foraging within sight and sound of each other. This happens both in and out of the breeding or rainy season (Figure 15).

The general picture regarding the temporal isolation of breeding is as follows: In parts of Africa where the rains fall for several months, sympatric bee-eaters allocate this favorable season between them; but where the annual rainy season lasts for only one or two months, the various species nest more or less at the same time (Figure 14).

With regard to diets, the Large Green specializes on Odonata, the Carmine on Orthoptera; the European is rather generalized and the White-throated somewhat aberrant; but all the other African *Merops* that have been investigated prey on the same spectrum of flying insects. The prey size seems to be roughly proportionate to the size of the predator, but the same 50 or so genera of insects occur repeatedly in nearly all the diets and comprise the greater part of the birds' food.

It could be that I am unduly influenced by having found, not once but repeatedly, several *Merops* species living and nesting close to each other in much the same habitat and exploiting exactly the same food resource. Perhaps further studies of the various species will show that ecological differences between them are more profound than appear at present.

## *Summary*

The bee-eaters (Meropidae) comprise a little-known palaeo-tropical family of 24 species. This paper reviews the sparse literature and presents new data on behavior, breeding biology, and food.

I have outlined the biology of the European Bee-eater (*Merops apiaster*), the only bee-eater that has received much attention in the past; and summarized my recent work, mainly on the African Red-throated Bee-eater (*M. bulocki*), under the headings Habitat and Evolution, Cooperative Breeding, and Bee-devenoming.

The 14 species that inhabit the savannas of Africa feed on insects caught in flight, mainly venomous Hymenoptera. They all eat honeybees (*Apis mellifera*), which comprise 2 to 96 per cent of their food numerically, and average 30 per cent. Diets are remarkably similar in the kinds of insects and the proportion of different kinds, except that the White-throated Bee-eater (*M. albicollis*) often takes grounded prey, the European (*M. apiaster*) has a generalized flying-insect diet, the Large Green (*M. superciliosus*) specializes on dragonflies, and the Carmine (*M. nubicus*) on locusts.

African savanna bee-eaters diverge in size — a weight factor of four — and plumage, although their structure and habits are rather uniform. They differ

somewhat in respect to habitat, preferred breeding season, and migration, but on the whole exhibit remarkably few ecological differences.

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# TIME-LAPSE PHOTOGRAPHIC RECORDS OF NESTING PEREGRINE FALCONS

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Biologists working on the Peregrine Falcon (*Falco peregrinus*) in the field have recently concentrated on trying to estimate the number of nesting pairs and their nesting success. With increasing frequency these surveys have revealed nests without eggs or young, nests with broken, addled, or thin-shelled eggs, or nests with dead young (Cade *et al.*, 1968; Enderson and Berger, 1968; Enderson *et al.*, 1968; Cade and Fyfe, 1970; Berger *et al.*, 1970). When Peakall (1970) suggested that abnormal parental behaviors induced by pesticides accompanied these reproductive failures, we realized that a detailed study of the Peregrine Falcon's nesting behavior was necessary.

Even though the numbers of Peregrine Falcons in interior Alaska have declined relatively little, the birds are producing thin-shelled, pesticide-laden eggs (Cade *et al.*, 1971). In the summer of 1970, from 8 June to 18 July, we followed the nesting biology of Peregrine Falcons at seven eyries along a 95-mile stretch of the Yukon River near the Alaska-Yukon Territory border, and, using time-lapse motion-picture cameras, recorded in detail the birds' nesting efforts. This report covers the nesting biology of five pairs that produced young and two pairs that failed. Our information on the overall nesting success of the Peregrine Falcons along the Yukon River in 1970 is included in an article by Cade and Fyfe (1970).

### *Methods*

We used single-frame, Super-8 Kodachrome II film in battery-powered, time-lapse motion-picture cameras with electronic timers that activated the shutters at predetermined intervals. Temple (1972) described the construction of these cameras. The cameras, timing mechanism, and batteries, fitted into a weatherproof metal box with a Plexiglas window, were set to operate at uniform intervals — between 2.5 and 3.5 minutes between frames at six nests and 5.5 minutes at the seventh, a difficult nest to visit. The film cartridges in the cameras, set between 2.5 and 3.5 minutes, lasted from six to seven days, long enough for us to make the circuit of the widely separated eyries.

The cameras, usually 1.5 to 2 meters from the clutch, were fastened to the cliff face with pitons (Figure 1). Aside from their initial attention after the installation of the camouflaged camera box, the falcons did not seem disturbed by the cameras. No female remained away from the eyrie more than 30 minutes after the installation, and, according to the films, the falcons were almost completely indifferent to the box; some even used it as a perch. The eyries we photographed produced young at a rate identical to that in the eyries that we checked only once at fledging time, further indicating that the cameras had no effect, adverse or otherwise. We operated the cameras from the third week of incubation to the fourth week of the nestling period. Table 1 gives the data on general nesting success as well as film coverage for each eyrie studied.

Because of the high latitude of the study area, where darkness rarely exceeds three hours a night and is usually much less, we lost little footage in each 24 hours. We edited the films frame-by-frame in a holder adapted to the stage of a 20× binocular microscope. The photographs reproduced here were copied from the films; in some, the area has been reduced.

## *Incubation*

### During Egg-laying

Since we began filming midway in incubation, we have no information on the egg-laying behavior of the Peregrine Falcon in Alaska. However, Enderson using the same photographic equipment in Colorado, in 1971, photographed a Prairie Falcon (*Falco mexicanus*) at the onset of laying. Beginning with the day the first egg was laid, the adults incubated the clutch for 15, 22, 64, 64, 90, and 90 per cent of the daylight hours through the next six days. The female was on the nest at dark and dawn on five of the six nights, suggesting that even before steady incubation begins, one bird often covers the eggs at night.

### Role of the Sexes

The male Peregrine Falcons contributed substantially to incubation (Table 2). During the period included in our films the males incubated one-third of the time with a tendency to participate less as hatching approached. This is a good deal more incubation by males than Cade's impressions (1960) indicated. In 29 per cent of the cases, the males were incubating at night when the light became inadequate for photography, quite unlike males at the Hudson River eyries that did not seem to incubate at night (Herbert and Herbert, 1965). Each sex spent about three attentive periods on the eggs each day. The males' periods averaged about two hours in length, the females' about four. We have only three pictures of a male and female together at an

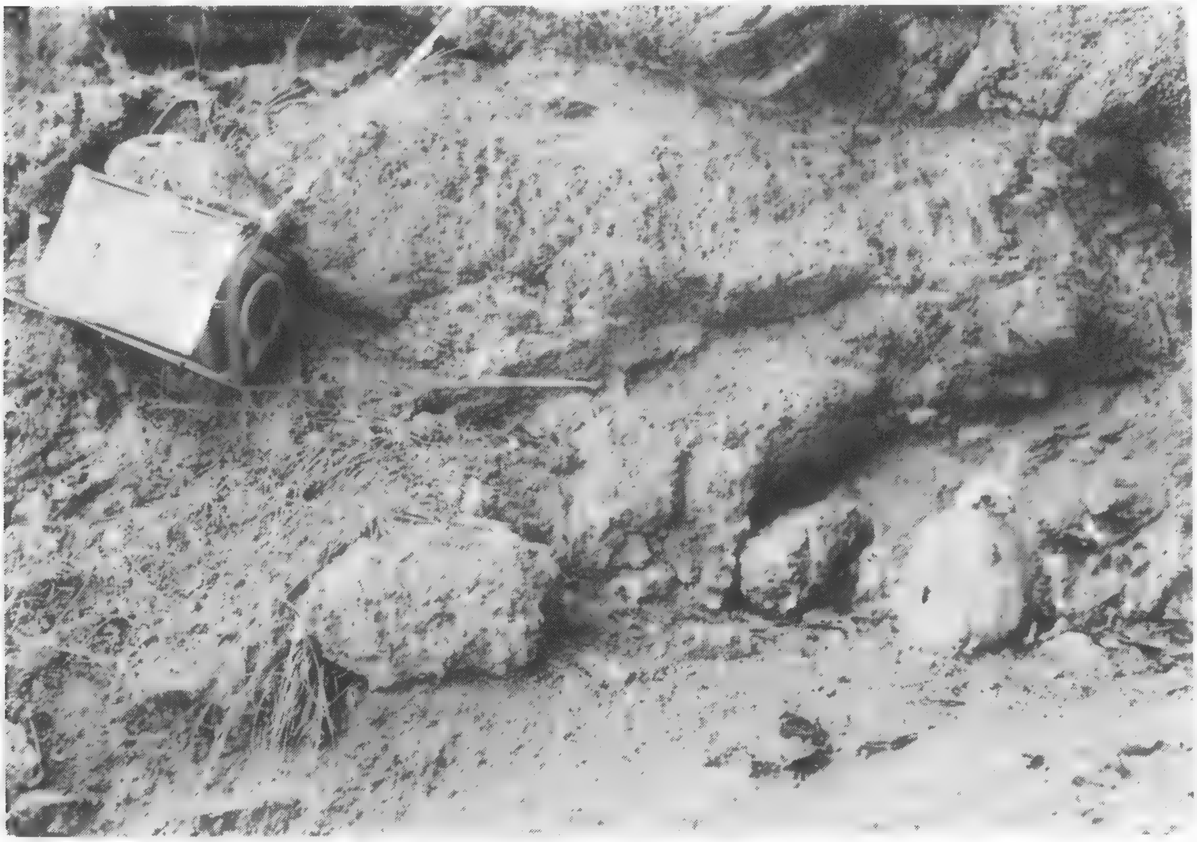


Figure 1. Camouflaged camera in operation about two meters from a Peregrine Falcon eyrie. The nestling is three weeks old.

## TABLE 1

### Film Coverage and Nest Contents of Peregrine Falcons

| *Eyrie number* | *Camera dates* | *Total frames** | *Film hours* | *Nest contents* | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | *Eggs laid*** | *Eggs addled* | *Eggs broken* | *Eggs hatched* | *Young fledged* |
| 1 | 8 June–15 July | 14,437 | 717 | 3 | 1 | 1 | 1 | 1 |
| 2 | 8 June–15 July | 14,990 | 694 | 4 | 0 | 0 | 4 | 3 |
| 3 | 9 June–10 June | 360 | 15 | 3 | 1 | 2 | 0 | 0 |
| 4 | 10 June–17 July | 9,081 | 861 | 4 | 0 | 0 | 4 | 3 |
| 5 | 11 June–17 July | 13,410 | 701 | 3 | 1 | 0 | 2 | 2 |
| 6 | 12 June–12 July | 4,352 | 498 | 3 | 1 | 2 | 0 | 0 |
| 7 | 16 June–18 July | 12,831 | 722 | 4 | 2 | 0 | 2 | 2 |
| Totals | | 69,461 | 4,208 | 24 | 6 | 5 | 13 | 11 |

*Excluding those lost at night.

**Eggs plus shell fragments on first visit.

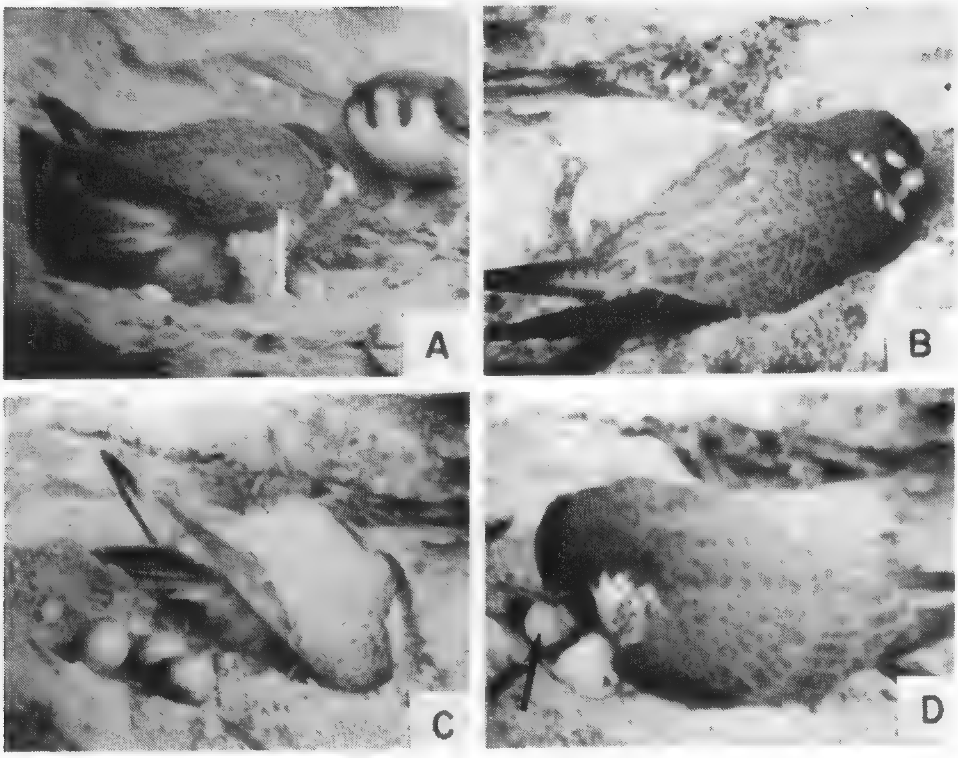


Figure 2. Time-lapse photographs of nesting Peregrine Falcons. (A) Adult male and female together at the eyrie briefly during nest relief. The male is entering on the right and the female on the left is just getting off the clutch. (B) Adult female incubating while asleep, or dozing, and with feathers on the back and rump erect. (C) An adult male in incubating posture next to the three-egg clutch. The bird is facing away from the camera and has apparently stretched out to reach something at the rear of the eyrie. (D) An adult female carefully removing a large fragment of freshly hatched eggshell from beneath her. The shell is indicated by an arrow and the newly hatched young is visible to the right of the shell fragment.

eyrie before hatching (Figure 2A), indicating that the exchanges at the nest occurred quickly.

### Inattentive Periods

The inattentive periods were short, averaging less than three minutes each (Table 2) and decreased in length as hatching time approached, supporting Cade's impression (1960) that the birds incubate most intensely just before hatching. Because our weekly maintenance visits kept the adults off the eggs for approximately 10 to 15 minutes and accounted for the longest inattentive periods, we caution anyone making routine nesting surveys of Peregrine Falcon eyries to make his visits as brief as possible during incubation.

### Behavior during Incubation

Changes in position and intermittent dozing characterize the falcons' behavior during incubation. At all seven eyries, the incubating bird changed position on an average of every 34 minutes (range of 24 to 53 for different nests). A marked increase in changes of position took place in the hours near hatching. If, as stated by Herbert and Herbert (1965), position changes are associated with egg-turning, then Peregrine Falcons move their eggs often, especially near hatching.

Dozing, a time when the incubating falcon had one or both eyes closed, occurred at any time of day. At three eyries where the cameras were in especially good position, the incubating female dozed in 16 per cent of the frames — range, 11 to 19 — and the males in 8 per cent — range, 8 to 9 (Figure 3C).

The incubating falcons often erected the feathers on the back and rump (Figure 2B). Though the function of this behavior is not clear, it may involve heat regulation. Obviously, the birds lose considerable body heat to the eggs and young by conduction.

### Unexpected Behavior

The cameras recorded some unexpected behavior during incubation. Now and then, an incubating adult picked up some debris in its bill, often stretching considerably in doing it and sometimes exposing the eggs. Perhaps because he had stretched too far, a male once sat in incubating posture beside the clutch for several minutes (Figure 2C). The only instance of an adult overlooking an uncovered egg occurred at night and lasted for about nine to 12 minutes. At one nest, two eggs that failed to hatch remained beside the nestlings for two weeks before they were trampled and broken. At another eyrie, the male noticed an addled egg nine days after the other eggs had hatched and carefully turned it. In the only recorded instance of an adult bringing prey to the eyrie during incubation, a female arrived with a male Pine Gros-

## TABLE 2

Attentive and Inattentive Periods in Incubating Peregrine Falcons

| *Days before hatching* | | 15–11 | 10–6 | 5–0 |
|---|---|---|---|---|
| *Number of eyries* | | 3 | 4 | 5 |
| *Male attentive periods** | *Number per day* | 3.0<br>(2.0–4.0) | 3.4<br>(3.1–3.7) | 2.7<br>(2.0–3.0) |
| | *Time in minutes* | 126<br>(121–132) | 136<br>(121–153) | 144<br>(97–203) |
| | *Per cent of total time* | 38.6<br>(32.1–45.1) | 34.1<br>(30.7–36.7) | 28.8<br>(15.4–41.1) |
| *Female attentive periods** | *Number per day* | 3.0<br>(2.0–4.0) | 3.6<br>(3.5–3.7) | 3.4<br>(3.0–3.8) |
| | *Time in minutes* | 244<br>(212–276) | 255<br>(192–265) | 245<br>(170–371) |
| | *Per cent of total time* | 60.4<br>(53.3–66.9) | 64.9<br>(62.3–67.9) | 70.6<br>(58.6–83.4) |
| *Inattentive periods*** | *Number per day* | 3.0<br>(2.0–4.0) | 2.5<br>(1.5–4.0) | 2.0<br>(1.0–2.4) |
| | *Time in minutes* | <3 | <3 | <3 |
| | *Per cent of total time* | 1.0<br>(0.5–1.6) | 1.0<br>(0.4–1.4) | 0.6<br>(0.3–1.2) |

*Mean for the indicated number of eyries; extremes in parentheses; excludes periods interrupted by darkness or field workers.

**Excluding periods resulting from our weekly maintenance visits.

beak (*Pinicola enucleator*) which she plucked and ate beside the clutch. This occurred on the day before hatching and may have been in response to the peeping of the embryos still inside the egg.

### Abnormalities

Except for the broken eggs and the failure of the remaining eggs to hatch, the events accompanying the reproductive failures at Eyries 3 and 6 had little in common (Table 1). For Eyrie 3, we have only 15 hours of continuous record due to a camera malfunction. During that time the female had 10 attentive periods and her inattentive periods averaged about six minutes each. The male had no attentive periods and appeared at the ledge in only one frame, a striking contrast to the activities of the males at the other six eyries.

At Eyrie 6, the pair incubated addled eggs until 8 July, 14 days after the last egg had hatched in the other eyries, yet all other aspects of incubation in this eyrie appeared to be similar to those in the successful eyries. The eggs were uncovered less than one per cent of the total time in the normal incubation period and only 4.5 per cent of the time during the following two weeks. Throughout the period the male attended the eggs 34 per cent of the total time, similar to males at successful nests (Table 2). When, 10 days beyond the normal hatching date, one egg broke, the female removed the broken egg and continued to incubate the lone egg. Four days later, after a normal attentive period, she left abruptly. Neither adult returned again to that eyrie.

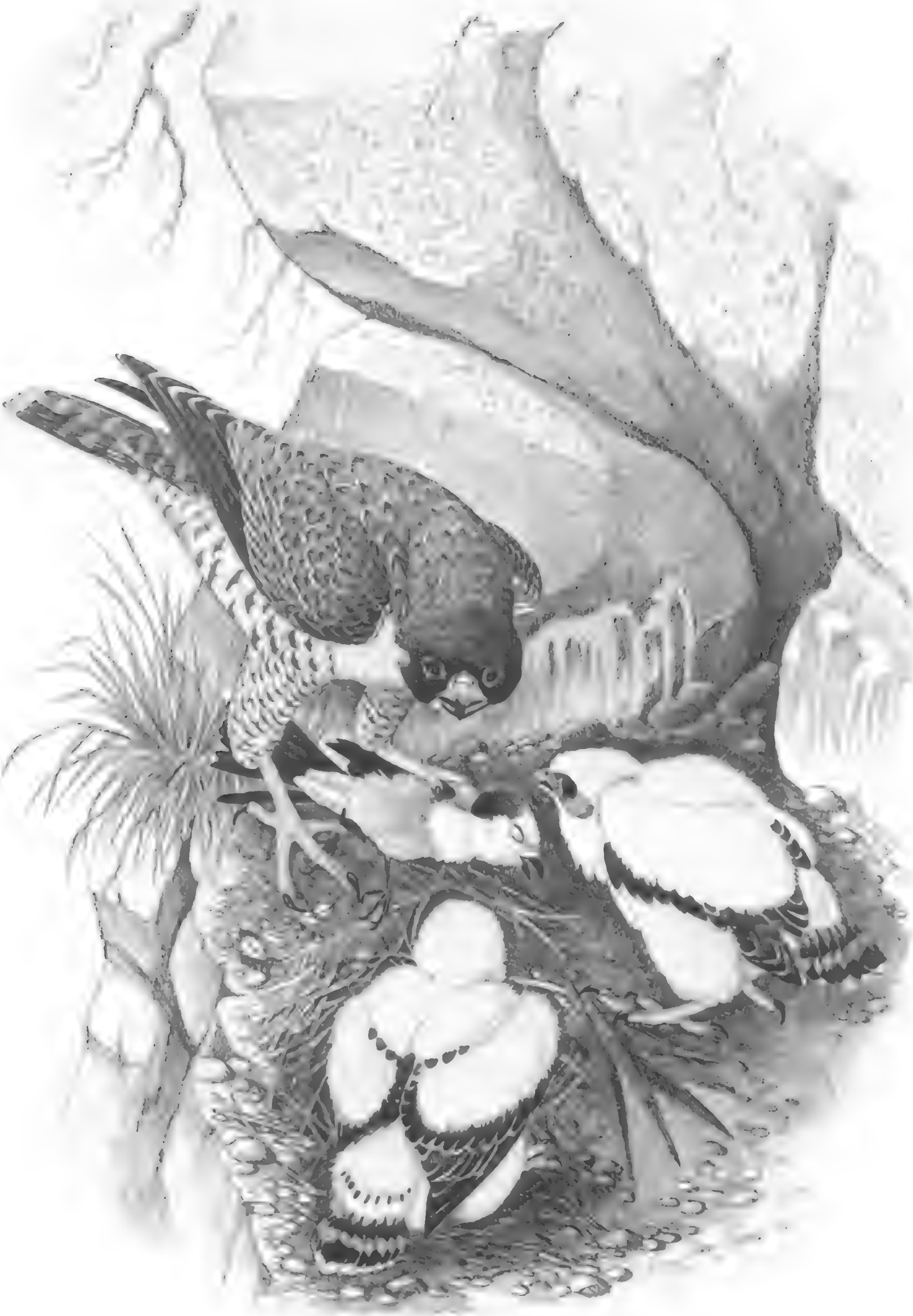
Except for the lack of attentive periods on the part of the male in Eyrie 3, our films of these unsuccessful pairs show no abnormalities of parental behavior to substantiate Peakall's suggestion.

Broken eggs occurred most frequently in Eyries 3 and 6 (Table 1). The mean thickness of fragments of four different shells from those nests was 0.216 millimeters (range, 0.203 to 0.233), measured without the membrane. Four shells from successful nests, measured in the same way, averaged 0.244 mm (range, 0.223 to 0.312). Porter and Wiemeyer (1969) showed that lowered hatching success accompanied thin eggshells in captive Sparrow Hawks (*Falco sparverius*) and Enderson and Berger (1970) found the same for wild Prairie Falcons.

## *Hatching*

The cameras recorded the synchrony of hatching at Eyries 4, 5, and 7. Only one young hatched in Eyrie 1, and at Eyrie 2 the camera was too distant for a count of newly hatched nestlings. At Eyrie 4 the two eggs hatched three hours apart; at Eyrie 7 the two hatched 28 hours apart, and at Eyrie 5, where four eggs hatched, the intervals after the first were 10 hours, between 60 and 72, and 110, respectively. The fourth nestling, probably unsuccessful in competition with older nestlings for food, died after four days. At Eyrie 2 the fourth young, much smaller than the rest, disappeared about 13 days after hatching, presumably for a similar reason.

In our pictures, the first indication that hatching was underway was the appearance of large fragments of eggshells from under the incubating female. She commonly picked them up (Figure 2D), but, unlike many species, did not remove them from the nest immediately. The males were not present during hatching at any of the nests.



Peregrine Falcon, *Falco peregrinus*. Drawing by Diane Pierce.

## *Brooding*

### Participation of Males

During hatching and thereafter, the participation by the males in the activities on the nest nearly ceased (Table 3). At four of the eyries, the only male activity was: Eyrie 5 — three feedings, three short brooding periods, one overnight brooding period, and several momentary appearances; no record of the male on the ledge after the nestlings were ten days old. Eyrie 4 — two short brooding periods, four momentary appearances, no feedings; no male recorded after the nestlings were six days old. Eyrie 1 — four periods each of feeding and brooding; male rarely recorded after the eighth day. Eyrie 7 — one feeding period, five short brooding periods; male recorded only once after the tenth day. When at the nest, the males most often merely stood near the young (Figure 3A) and rarely assumed full brooding posture. In contrast to these records, we have the report by Heatherley (1913) on a single eyrie where the male participated frequently in the care of the nestlings.

TABLE 3

Participation of Sexes in Care of Nestling Peregrine Falcons

| | *Per cent of total brooding time** | *Per cent of total feedings present** | *Per cent of total time present** |
|---|---|---|---|
| Male | 1.2 (0.6–1.8) | 3.7 (0.0–8.3) | 2.2 (0.7–3.5) |
| Female | 98.8 (98.2–99.4) | 96.3 (91.7–100.0) | 97.8 (96.5–99.3) |

*Mean for four eyries from hatching to 25 days later; extremes in parentheses.

### Brooding Attentiveness

The females brooded the young Peregrine Falcons steadily during their first week, interrupting their brooding only to receive food from the males and feed the nestlings and themselves. Figure 4 shows the brooding attentiveness through the first 25 days of the nestling period. Since the five broods were up to nine days out of phase with respect to hatching dates, the extremes in daily ambient temperatures affected the need for brooding differently at different eyries. Using the maximum and minimum daily temperatures, wind, and rainfall data from the U. S. Weather Bureau at Eagle, Alaska, centrally located in the study area, we found correlations between the mean daily temperatures and the percentage of brooding time (Figure 4).

The nestlings at all five eyries were brooded over 90 per cent of the time during the first three days after the mean hatching date, and over 80 per cent during the first eight days. After the third day, nearly all decreases in brooding time occurred on days when the mean daily temperature was at least four Fahrenheit degrees above 58, the mean for the entire 25-day period. Conversely, after the nestlings were two weeks old, increased brooding was generally associated with mean daily temperatures below the average for the period (Figure 3E). In general, the females brooded the nestlings over 90 per cent

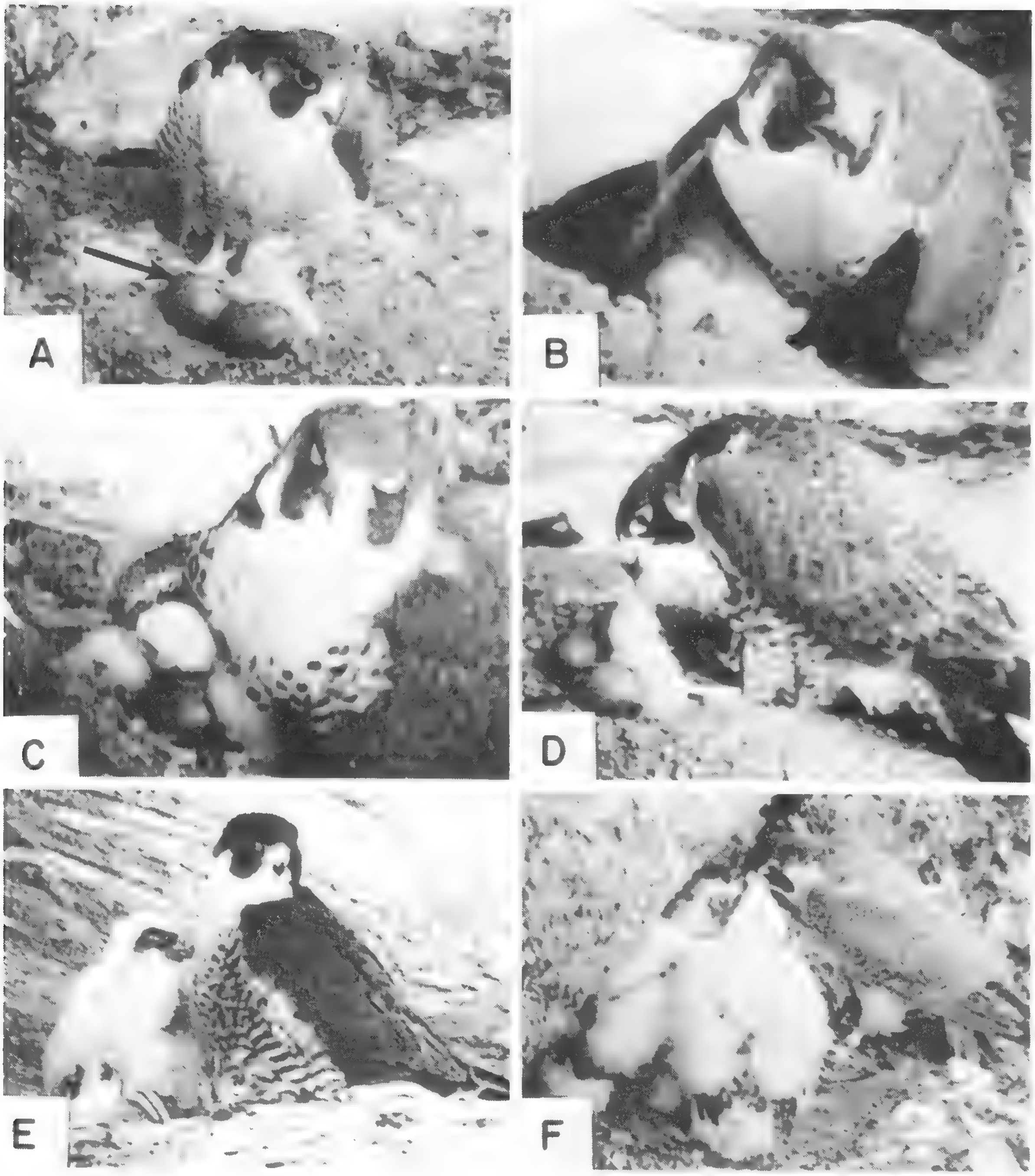


Figure 3. Time-lapse photographs of nesting Peregrine Falcons. (A) An adult male in a characteristic partial brooding posture. Note the pipped egg, indicated by an arrow, and the newly hatched young to the right. The open-mouthed young is holding its head up in a food-begging posture. (B) An overheated adult female panting in the midday sun while brooding two one-week-old nestlings. (C) Two one-week-old nestlings with their heads protruding from beneath the dozing, brooding female. (D) A four-hour-old young raising its head to receive its first meal from the adult female. Note the two unhatched eggs next to the young. (E) An adult female brooding a sleeping three-week-old nestling during a cold rainstorm. This nestling received no such attention immediately before or after the storm. (F) An adult bill-feeding two large nestlings three-and-one-half weeks old. Even at this age, when nearly as large as the adults, nestlings rarely feed themselves.

of the time on Days 1 through 6, about 88 per cent by Day 10, 60 per cent by Day 15, 40 per cent by Day 17, and under 10 per cent by Day 20.

From 1–5 July, the mean daily temperatures were between four and eight degrees above average and included the highest recorded temperatures of the study period. In that five-day interval, the brooding time dropped to a minimum average of about 40 per cent for the five pairs even though the youngest brood was only 11 days old. In the next three days, 6–8 July, the warm period ended abruptly with continual rain and an average drop of one degree in mean temperature below the period mean. In these three days the youngest nestlings, 14 days old, were brooded a maximum of 92 per cent of the total time on one day, and the oldest nestlings, 21 days old, were brooded 35 per cent of the time, a marked change from the less than 10 per cent brooding attentiveness that the oldest brood received before and after that time.

Of the five eyries, two faced northeast, two faced southeast, and one faced south. Only at the eyrie with the southern exposure did we have evidence of overheating of the young or brooding adult in the midday sun. The adult panted while shading the young (Figure 3B). On our first visit to change the film after the young had hatched, the female left the four four-day-old nestlings about 17 minutes before we reached the ledge, and, in the short time it took us to get there, the young became so overheated and uncomfortable that they crawled from the sunny nest depression toward the shade of the ledge. By the time these young were nine days old, they had permanently deserted the nest depression for the more shaded corners of the eyrie.

Perhaps because of the vagaries of cloud cover, chilly winds, and rain, our data show little evidence of a daily rhythm during the second week after hatching when the chicks did not require constant brooding (Figure 5). The adults were only slightly more attentive to the young in the hours just before and just after midnight. The nestlings in Eyrie 2, the only eyrie containing four nestlings at that time, consistently received the least attention.

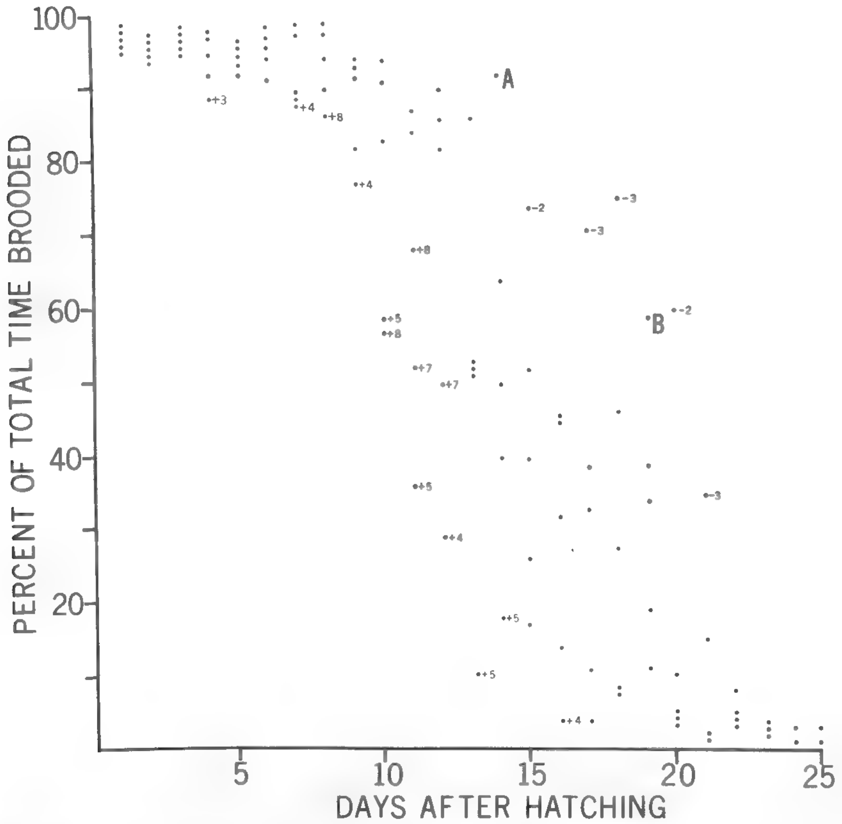


Figure 4. Brooding attentiveness of Peregrine Falcons during the first 25 days after hatching. The numbers show plus or minus deviations in degrees Fahrenheit from average mean daily temperature for the period from mid-June to mid-July. Two factors tending to increase the brooding time were (A) rain falling on nest ledge and (B) occurrence of lowest maximum daily temperature for the period.
]

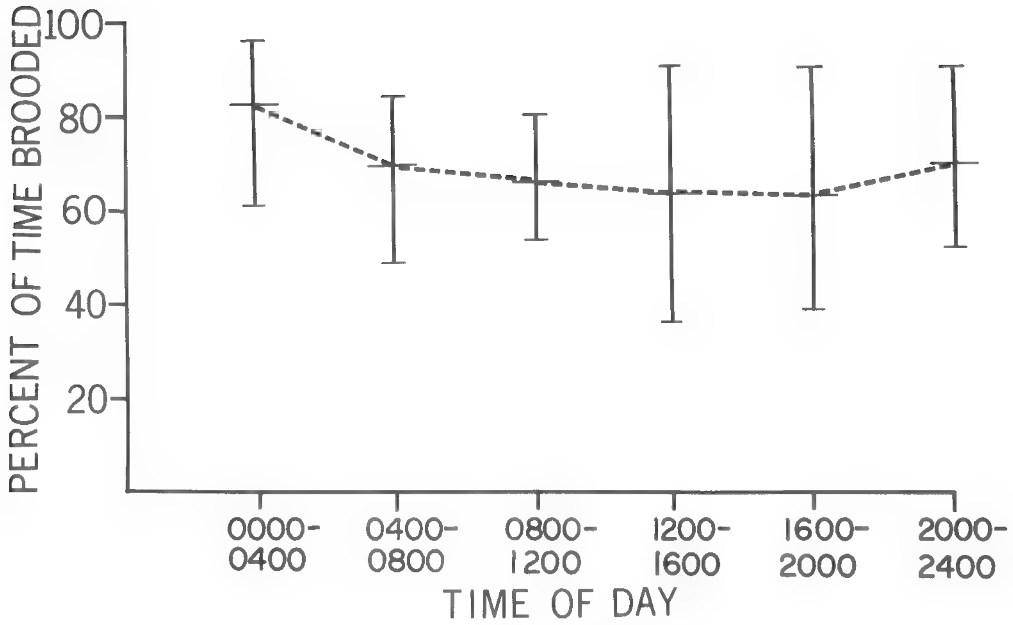


Figure 5. Daily brooding rhythm at five eyries during the second week after hatching. The vertical lines represent ranges, dashed line connects means.

Nestlings less than a week old often pushed themselves out from beneath the brooding adult (Figure 3C). At Eyrie 5, one or both of the two were visible 31 per cent of the time on the third day after hatching when the mean daily temperature was two degrees below the mean for the study period. During the first seven days after hatching, the single nestling in Eyrie 1 was visible beneath the brooding adult 1, 1, 3, 8, 18, 25, and 35 per cent of each respective day. Since there were no unusual temperature variations during this period, the increase in nestling exposure may have reflected the chick's thermoregulatory development. In captivity, artificially brooded Peregrine Falcons of this age give a characteristic call when they are cold. Possibly sound recordings will reveal the respective roles of nestlings and adults in maintaining proper brooding temperatures.

## *Feeding and Diet*

The adults may feed the nestling Peregrine Falcons very soon after hatching. One young was first fed when it was only four hours old (Figure 3D). At four eyries where we knew the exact time of hatching, the adults fed the nestlings within four to eight hours. After the first feeding, the average number per day increased to between two and three per nestling except in Eyrie 1 where the lone nestling ate more often (Table 4).

The time between feedings was initially about eight hours and this interval was almost halved by the end of the first week. We found no close correlation between the length of each feeding and the number of nestlings in the eyrie; each feeding generally required ten minutes. This agrees closely with observations of European Peregrine Falcons by Heatherley (1913). Young nestlings apparently took longer to eat less so that the time per feeding was fairly constant.

Not surprisingly, the frequency with which the adults brought food to the ledge showed a positive correlation with the number of young in the nest

(Figure 6). However, the slope of this curve is shallow, indicating that nestlings in smaller broods had more food available to them.

In general, self-feeding by nestlings was not at all important at any of the five eyries during the filming (Figure 3F), a fact contrary to observations of Peregrine Falcons on the Hudson River (Herbert and Herbert, 1965). At Eyrie 5, where our film record is complete for 31 days after hatching, the camera recorded a nestling feeding itself only once, on Day 28. At Eyrie 7, the young merely held the prey remains in their feet or bills on Days 16 and 19.

## Nestling Diet

At Eyries 1, 4, 5, and 7, where the cameras were close enough for the identification of prey, 502 feedings took place. Unfortunately, the prey items brought to the eyries were either too well plucked for identification or the adults or nestlings obscured the view. From the 502 feedings we identified only 13 items: three small ducks, one Sharp-shinned Hawk *(Accipiter striatus)*, one Solitary Sandpiper (*Tringa solitaria*), one Yellowlegs (*Totanus* sp.), two shorebirds, two Yellow-shafted Flickers (*Colaptes auratus*), one Pine Grosbeak, one Gray Jay (*Perisoreus canadensis*), and one small passerine. The

TABLE 4

Rates of Feeding of Nestling Peregrine Falcons

| *Days after hatching of first egg* | *Number of eyries* | *Feedings per nestling per day**† | *Time between feedings (minutes)** | *Time for each feeding (minutes)** |
|---|---|---|---|---|
| 0–2 | 5 | 1.9<br>(0.8–3.0) | 480<br>(270–864) | 9.2<br>(7.0–12.2) |
| 3–5 | 5 | 2.6<br>(1.3–3.7) | 282<br>(188–393) | 10.2<br>(6.4–14.1) |
| 6–8 | 5 | 2.8<br>(2.0–4.6) | 253<br>(180–332) | 11.1<br>(8.4–15.7) |
| 9–11 | 5 | 2.7<br>(1.6–5.0) | 267<br>(227–308) | 10.5<br>(7.3–14.8) |
| 12–14 | 5 | 2.8<br>(1.6–4.7) | 255<br>(227–308) | 10.5<br>(8.5–13.5) |
| 15–17 | 4 | 2.4<br>(1.3–3.7) | 336<br>(288–393) | 11.7<br>(7.8–15.9) |
| 18–20 | 4 | 2.0<br>(1.4–2.7) | 305<br>(270–332) | 11.6<br>(10.1–13.2) |
| 21–23 | 4 | 2.4<br>(1.4–4.3) | 321<br>(288–332) | 8.5<br>(6.2–10.4) |
| 24–26 | 3 | 2.6<br>(1.4–4.8) | 355<br>(300–432) | 10.2<br>(7.4–12.7) |
| 27–29 | 1 | 1.8 | 400 | 10.2 |

*Mean for the indicated number of eyries; range in parentheses.

†Except for Days 18–20, the upper limit of the range was for an eyrie with one young.

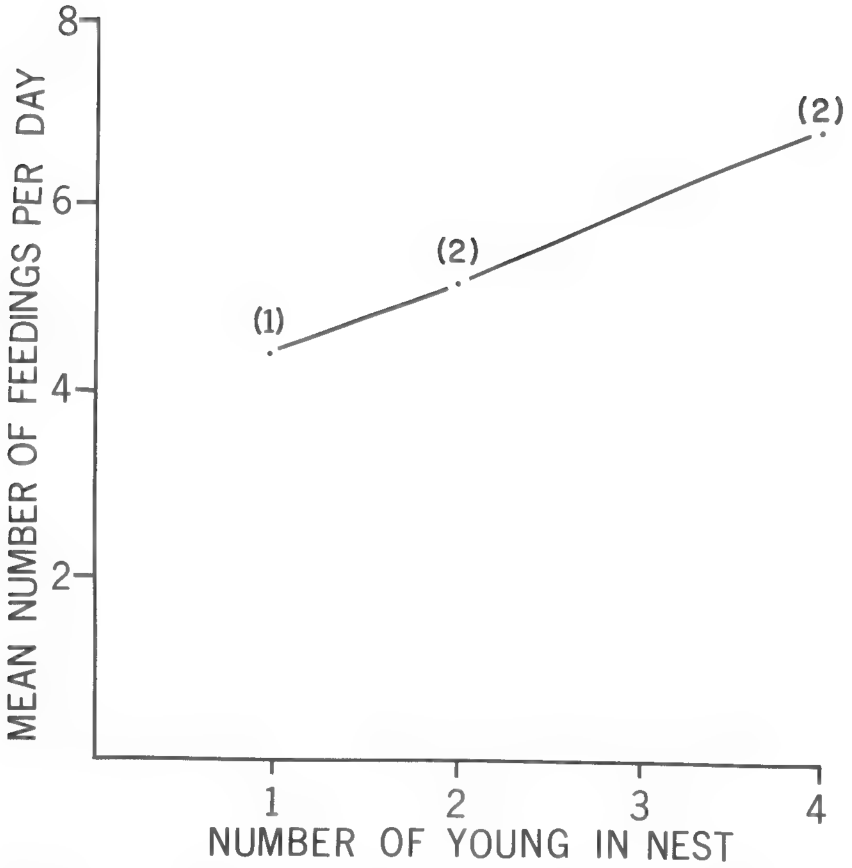


Figure 6. Relationship between number of young and frequency of feeding during the first two weeks of the nestling period. The numbers in parentheses are numbers of broods represented. The two broods with four young lost one young each, one dying at four days and the other at 13 days.

Sharp-shinned Hawk is the only addition to the long list of prey of the Yukon River Peregrine Falcons given by Cade *et al.* (1968).

Never did we record an adult leaving the remains of a prey on the ledge after it had fed the young. The adult always carried off all parts not eaten by the nestlings. Nor have we any evidence of the transfer of food between the adults on the nest ledge; such exchanges apparently occurred elsewhere.

## *Molt Patterns of Nesting Peregrine Falcons*

The films provided information on the molt of the primaries and rectrices of four adult males and five adult females. The molt of the rectrices had not begun in any of the birds by mid-July. In the molt of the primaries, Pair 1, the innermost, although it does not show in most of the photographs, was among the first of three pairs to be molted in one male and two females. There was no variation between the sexes in the molt sequence at this time. By mid-June, Pair 4 of the primaries was nearly replaced and Pair 5 was about half-grown; by mid-July, Pair 1 had been dropped and replaced and Pair 5 was almost full grown. In early July, females ceased molting the primaries and were fully feathered with old and new primaries. This coincided with the time when they resumed hunting to provide food for the nestlings. By 18 July, after having a full complement of primaries for over two weeks, one female had resumed the molt, dropping Primaries 3 and 6.

The molt of the primaries in the males differed from that in the females. None of the feathers distal to Pair 4 had molted by mid-June and none had molted by 4 July, our latest date for information on the molt of the males. Primaries 3 and 4 were in various stages of replacement in two males in mid-June; one male had replaced the first three pairs by that time, and another had dropped no primaries from Pair 2 outward. It is not surprising that the molts of the males and females are different at this time in view of their vastly different roles in the care of the young.

## *Conclusion*

We feel that the time-lapse cameras were successful in recording certain aspects of the nesting biology of the Peregrine Falcon. When one considers the difficulty in reaching most eyries, the time involved, and the disturbance that even brief visits cause, we know that we disturbed the birds less and we obtained a great deal more information than we could possibly have gathered without them in many summers. The films are important, if for no other reason, in that they have made us aware of the very short inattentive periods during incubation, a sharp warning to all biologists studying or censusing Peregrine Falcons never to linger at an eyrie at that stage. They have also given us some insight on such matters as movement of eggs, brooding, and feeding that may help us in trying to rear Peregrine Falcons in captivity.

There is probably a lot of information still hidden in our 70,000 frames of film. Although we have noticed no abnormalities in parental behavior at the unsuccessful nests, as Peakall (1970) suspected, we may yet uncover some clues that so far we have overlooked. At least, we have pictorial records of five normal nests — one that produced one young, two that produced two, and two that produced three — for future comparisons.

## *Summary*

From 8 June to 18 July 1970, about two weeks before hatching to four weeks after hatching, we photographed with automatic, time-lapse motion-picture cameras the nesting activities of seven pairs of Peregrine Falcons (*Falco peregrinus*) on the Yukon River near the Alaska-Yukon Territory border. With intervals between photographs as short as 2.5 minutes we obtained nearly 70,000 pictures representing 4,200 film hours.

The adult males ordinarily incubated about one-third of the time. Their attentive periods lasted between two and three hours; the females' attentive periods lasted about four hours. Except at one eyrie where the eggs failed to hatch, the inattentive periods accounted for less than one per cent of the total time, each lasting less than three minutes.

The incubating adults changed position on an average of every half hour and may have shifted the eggs with each change. If this is so, we know that the eggs of the Peregrine Falcon are moved frequently.

Two nests failed to produce young. In both cases the eggs were broken and the shell fragments, when measured, were thinner than those at the successful eyries. The male in one nest that failed never incubated and appeared on the ledge of the eyrie in only one frame of the 15-hour film sequence. Since the female's attentive periods were shorter and her inattentive periods longer than those at the other eyries, the male had plenty of opportunities to incubate.

The males seldom visited the eyries after hatching; the females brooded the nestlings almost exclusively, about 90 per cent of the time during the first week and after that reduced their brooding time so rapidly that at the end of the third week they brooded less than 10 per cent of the time. Although lower than average ambient temperatures increased the average brooding time at one period, the females maintained a slight daily brooding cycle — most intense before and after midnight and least intense in the late afternoon.

The female fed the young within a few hours after hatching and continued with a frequency that reached once every four to five hours, with about 2.5 feedings per young per day. The nestling Peregrine Falcons rarely fed themselves or even tried to do so.

The molt patterns of the adults are correlated with the nesting behaviors of the sexes. The females stopped molting for several days in early July, but each one always had a full complement of primaries, some old and some new. The males varied in the order of molt of the first four pairs of primaries; we have no records of the replacing of their more distal feathers. The females showed a consistent pattern involving the primaries farther out on the wing.

### *Acknowledgments*

The National Audubon Society supported our photographic study of the nesting biology of the Peregrine Falcon, and the University of Alaska provided logistic assistance during our time in the field.

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# WINTERING WARBLERS IN JAMAICA

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Photographs by the authors

Ecological isolation in the breeding season has been shown for species in many families of birds, but few data are yet available for migrants in winter quarters (Lack, 1971). The warblers of the family Parulidae present a special challenge in this respect, since so many of them winter in the same area, and most of them are separated ecologically in summer in subtle ways (MacArthur, 1958). During our stay in Jamaica, from mid-October 1970 until well after the warblers left in the summer of 1971, we studied their habitats, feeding stations, and feeding methods, but not their actual food. Because, so far as we could see, no species in other families share ecological niches with the Parulidae, we limited our study to the members of this family.

Thirty-five passerine species breed in Jamaica; of these four are mainly or exclusively summer visitors. The 31 resident species, which include two parulid warblers, are joined in winter by 18 other parulids and two other passerine species from North America. Hence, visitors comprise two-fifths of the passerine species present in winter — and roughly one-quarter of the individuals of all passerine species that we saw. The parulid species concerned, with two measurements from Ridgway (1902), appear in Table 1 with the resident Jamaican species first.

## *Methods and Localities of Study*

### Methods

We made three types of counts (Table 2): (1) slow walks through the forest, (2) quick walks through the forest, and (3) fairly slow walks along trails at the forest edge.

On slow walks through the various habitats we stopped to record the manner of feeding when we saw it. Our walking speed was roughly 0.8 kilometer per hour, but we did not attempt to keep our speed uniform and it varied somewhat with the birds seen feeding and other conditions. We recorded only the individual birds seen. Such counts, while superior to a simple record of "common," "rare," etc., are difficult to relate to the density of birds per unit area for the following reasons.

First, because warblers are much more in evidence soon after dawn than later in the day, we made all our counts in early morning. But the decline in warbler activity later in the day is much greater in some habitats, notably the

## TABLE 1

The Warblers in Jamaica

| *Species* | *Mean wing* length (mm)* | *Mean culmen* length (mm)* |
|---|---|---|
| *Resident* | | |
| Yellow Warbler, *Dendroica petechia* | 65 | 10.6 |
| Arrow-headed Warbler, *Dendroica pharetra* | 63 | 11.3 |
| *Wintering*** | | |
| Black-and-white Warbler, *Mniotilta varia* | 69 | 11.4 |
| Swainson's Warbler, *Limnothlypis swainsonii* | 70 | 15.0 |
| Worm-eating Warbler, *Helmitheros vermivorus* | 69 | 13.7 |
| Tennessee Warbler, *Vermivora peregrina* | 65 | 9.6 |
| Parula Warbler, *Parula americana* | 61 | 9.9 |
| Magnolia Warbler, *Dendroica magnolia* | 60 | 9.0 |
| Cape May Warbler, *Dendroica tigrina* | 66 | 9.8 |
| Black-throated Blue Warbler, *Dendroica caerulescens* | 65 | 9.4 |
| Myrtle Warbler, *Dendroica coronata* | 74 | 10.0 |
| Black-throated Green Warbler, *Dendroica virens* | 64 | 9.9 |
| Yellow-throated Warbler, *Dendroica dominica* | 67 | 13.8 |
| Prairie Warbler, *Dendroica discolor* | 58 | 9.4 |
| Palm Warbler, *Dendroica palmarum* | 65 | 9.9 |
| Ovenbird, *Seiurus aurocapillus* | 73 | 11.7 |
| Northern Waterthrush, *Seiurus noveboracensis* | 77 | 12.7 |
| Louisiana Waterthrush, *Seiurus motacilla* | 81 | 13.2 |
| Common Yellowthroat, *Geothlypis trichas* | 53 | 10.5 |
| American Redstart, *Setophaga ruticilla* | 64 | 8.5 |

*Measurements of adult males (Ridgway, 1902).

**Two regular wintering species, Tennessee Warbler (*Vermivora peregrina*) and Myrtle Warbler (*Dendroica coronata*), omitted from other tables and analyses because they are too scarce to warrant quantitative assessment.

arid lowland forest, than in others such as the montane forest. Second, since the vegetation in the Jamaican forest is dense and many slopes are too steep for walking, one can census carefully only along tracks, which vary in width. Wide tracks make visibility in the forest canopy easier; narrow tracks help the observation of birds on the ground. Further, some forests have tracks only along the edge, making it easy to see birds of the forest edge and difficult to see birds on the forest floor. Finally, a quick walk is better than a slow one for seeing the shy, ground-feeding species which usually spot a strolling observer farther away and slip off unnoticed.

We observed the Swainson's Warbler and Ovenbird, both ground-feeding species, more often on quick walks than slow ones, and the Common Yellowthroat, a herb-feeding species, most often along the forest edge. All the rest, the tree-feeding species, were equally common on all three types of counts

(Table 2). A comparison of the birds seen with those caught in mist nets, extending from the ground to a height of two meters, revealed similar differences (Table 3). Although a comparison of birds seen with those caught on Port Henderson Hill in the lowland arid region shows no pattern comparable to the patterns in other areas, this may be due to the extremely low canopy caused by forest clearance. In the three other areas, we netted a much higher proportion of ground and shrub-feeding species than we saw, and we saw a greater proportion of tree-feeding species than we netted. Table 3 shows this crudely. The difference is particularly marked in the ground-feeding Swainson's Warbler and Ovenbird, the low-feeding Worm-eating Warbler, and the tree-feeding Parula, Yellow-throated, and Prairie Warblers.

The number of observers may also affect the number of birds seen per unit of time. On slow walks through montane forest near Hardwar Gap with one, two, three, and four observers, the average number of warblers recorded

## TABLE 2

Variation in Number of Warblers Seen in Jamaica under Different Conditions*

| *Species*** | *Number of birds per 10 hours* | | |
|---|---|---|---|
| | *Slow walks† through forest* | *Quick walks† through forest* | *Fairly slow walks on roadside edges of forest* |
| *Resident* | | | |
| Arrow-headed | 21 | 18 | 19 |
| *Wintering* | | | |
| Black-and-white | 13 | 11 | 12 |
| Swainson's | 3 | 6 | 0 |
| Worm-eating | 1 | 1 | 1 |
| Black-throated Blue | 7 | 7 | 8 |
| Ovenbird | 2 | 6 | 1 |
| Common Yellowthroat | x†† | 2 | 11 |
| American Redstart | 1 | 0 | 2 |
| Total warblers (including a few warblers not listed above) | 50 | 53 | 61 |
| Total passerines | 138 | 120 | 265 |
| Number of hours | 32 | 9 | 12 |

*Montane forest, near Hardwar Gap, 1,200 meters elevation.

**Commonest warblers.

†Slow walks, about 0.8 km per hour; quick walks, about 3.2 km per hour. Difference on slow walks and quick walks between Swainson's Warbler and Ovenbird and all the rest, except the Common Yellowthroat, is statistically significant ($x^2 = 10.98$, $P < .01$).

††Present but less than 0.5 per 10 hours.

per hour was 5.6, 4.1, 6.4, and 6.9, respectively; these differences are not statistically significant. In thick forest, two observers only a few feet apart often see different individual birds, partly because each tends to watch in a somewhat different direction and partly because, even when looking in the same direction, each has a different view through the cover.

Differences, occasionally large, occur in the number of warblers seen on different days in the same place, between the same times, and by the same observers. We noted the biggest difference along a narrow road in a good secondary forest at Ferry River where the same three observers counted from 08:00 until 10:30 on 15 and 27 January. On the first walk, they saw 24 parulids and 44 individuals of other passerine species; on the second, 48 parulids and 17 individuals of other passerines. We believe that a wind on the second walk may have depressed the activities of the other passerines, but we cannot explain the increase in the number of parulids. Thus, one must exercise great caution in interpreting the differences in the numbers of birds observed.

We recorded feeding height only once for each individual — at the time when we first saw it feeding; we noted its manner of feeding for up to five successive times when we could follow it. After the fifth observation we turned to another individual. Because some types of feeding are far more conspicuous than others — a warbler snatching insects in the air is far easier to see than a warbler gleaning insects from a leaf — the recorded proportions of each type of feeding may be somewhat biased.

## Habitats

The vegetation of Jamaica includes four main types of natural forest and woodland — mangroves, lowland dry limestone forest, midlevel wet limestone forest, and montane shale forest (Asprey and Robbins, 1953). Mangroves, which are not extensive except in Kingston Harbour, usually form a relatively narrow strip. We made censuses in mangroves along the south coast near Morant Point, Morant Bay, Kingston Harbour, and the edges of the Hellshire Hills and Portland Ridge.

Lowland dry limestone forest is variable. We censused at sea level at Morant Point and Negril. There has been a great deal of clearing in both areas which were apt to be flooded. We often counted in the extremely arid scrub forest, still in its natural state except for a few trails, in the Hellshire Hills (Figure 1) and on Portland Ridge and in similar but heavily cut-over forest on Port Henderson Hill. Less arid, cut-over scrub forest covers much of the southern lowland hills, where we censused on Long Mountain near Mona. We worked frequently in the relatively rich secondary woods at an altitude of 60 to 120 meters above Ferry (Fresh) River, west of Kingston, and in secondary riverine woodland with taller trees along the Ferry River and beside the stream from Mona Reservoir. We worked in a tall natural riverine forest in Fern Gully in the north.

We counted in midlevel forest mainly on Mount Diablo above Worthy Park where we had to observe mostly from grassy pastures at the edge and thus saw very few ground-feeding warblers. We also made a few counts in the natural forest of the Cockpit Country (Figure 2) and at Dolphin Head. We counted in montane forest mainly between Catherine's Peak and Middleton Mount, near Hardwar Gap, between 1,200 and 1,500 meters above sea level, and several times along the higher trail from St. Helen's to Morce's Gap (Figure 3).

## TABLE 3

### Comparison of Warblers Seen and Mist-netted in the Same or Similar Areas in Jamaica

| *Species* | *Percentages of birds recorded** | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Lowland*** *arid* | | *Lowland**** *riverine* | | *Middle*† *elevation* | | *Montane*†† | |
| *Residents* | | | | | | | | |
| Yellow | 12 | — | — | — | — | — | — | — |
| Arrow-headed | — | — | — | — | 8 | 21 | 28 | 18 |
| *Wintering* | | | | | | | | |
| Black-and-white | 18 | 38 | 21 | 10 | 21 | 18 | 16 | 10 |
| Swainson's | — | — | 1 | 5 | — | 2 | — | 5 |
| Worm-eating | — | — | x‡ | 7 | — | 11 | 1 | 15 |
| Tennessee | — | — | 2 | 2 | — | — | 1 | — |
| Parula | 9 | 7 | 10 | 5 | 4 | 2 | 2 | — |
| Magnolia | — | — | 4 | 2 | — | — | 1 | — |
| Cape May | — | — | 2 | — | 12 | 10 | — | — |
| Black-throated Blue | — | — | 7 | 7 | 25 | 11 | 17 | 21 |
| Myrtle | — | — | — | — | — | — | — | — |
| Black-throated Green | — | — | 4 | 1 | 7 | 6 | 8 | 8 |
| Yellow-throated | — | — | — | — | 5 | 1 | 2 | — |
| Prairie | 26 | 33 | 14 | 3 | 9 | 4 | 1 | — |
| Palm | 9 | — | — | — | 1 | 3 | 3 | — |
| Ovenbird | 15 | 13 | 3 | 12 | 3 | 7 | 1 | 8 |
| Northern Waterthrush | — | — | 5 | 7 | — | — | — | — |
| Louisiana Waterthrush | — | — | — | — | — | — | 3 | — |
| Common Yellowthroat | 12 | — | 15 | 33 | 3 | 1 | 12 | 10 |
| American Redstart | — | 9 | 12 | 5 | 2 | 2 | 3 | 5 |
| Total warblers | 34 | 55 | 248 | 136 | 126 | 90 | 138 | 39 |

*First figure is percentage of birds seen only; second figure is percentage of birds netted. Of the 6 ground-feeding and low feeding species, 47 individuals were seen, 123 netted. Of the 11 tree-feeding species, 248 individuals were seen, 172 netted.

**Port Henderson Hill: Extremely arid area of abnormally low natural scrub forest; totals not included in main counts for lowland limestone forest in Table 4 because of heavy cutting by charcoal burners.

***Near Mona Reservoir: 150 meters elevation with stream and mimosaceous trees; somewhat disturbed by cutting.

†Irish Town: Netting in wild garden with adjoining woodland and cultivated land at 600 meters elevation; census at Guava Ridge, many more conifers, 1,200 meters elevation.

††Green Hills: Netting at field station of Institute of Jamaica, overgrown wild garden adjoining montane forest; census through garden, forest, and at Hardwar Gap, 1,100 to 1,200 meters elevation.

‡Seen outside counts.

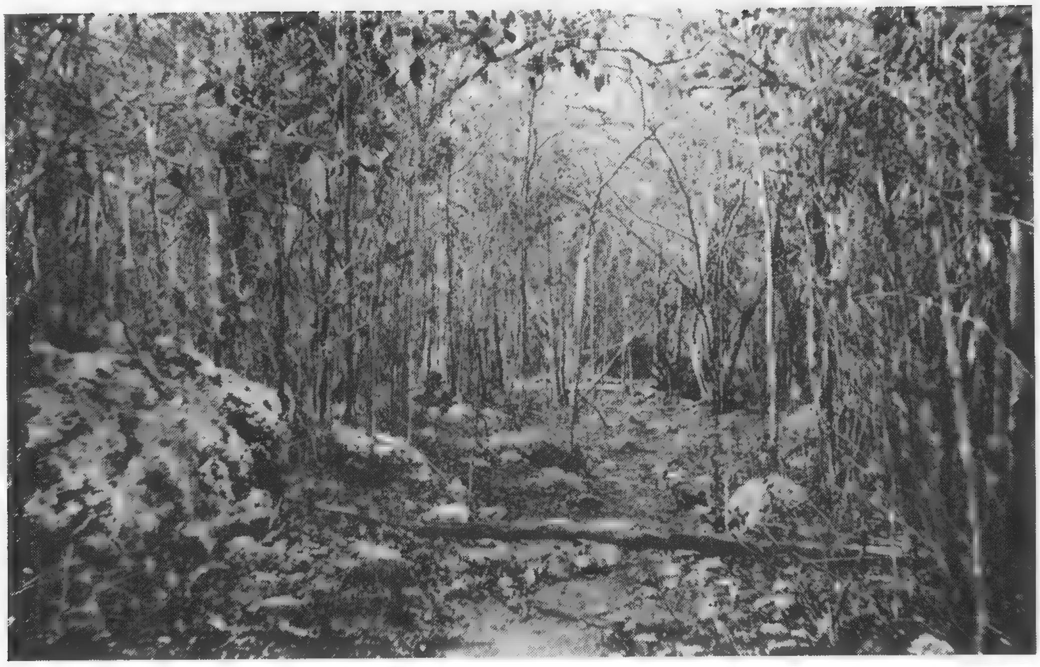


Figure 1. Lowland dry limestone forest (xeric scrub forest) in the Hellshire Hills, Jamaica.

We counted in all the main natural habitats except river swamps with sedges, where Northern Waterthrushes and Common Yellowthroats are the only common warblers. We also censused five wooded habitats much modified by man: the Royal Botanical Garden in Kingston, the midlevel woods around the Hermitage Reservoir at 500 to 600 meters elevation, Guava Ridge at about 1,200 meters, Holywell Picnic Site at Hardwar Gap, and Cinchona Botanic Garden at 1,400 meters. Although these five places have many wintering warblers, artificial habitats occupy such a small part of Jamaica that the majority of the wintering warblers live in natural, though often partly cleared, forest. We did not census agricultural areas of sugar cane, coconuts, bananas, or citrus fruits where warblers are scarce. Nor did we census in grassy pastures where the only parulid is the Palm Warbler, usually found near trees and bushes.

The summary of our censuses in Table 4 shows that most of the wintering warblers occur in both lowland and montane forest, and that habitat separates hardly any. Two exceptions are the waterthrushes and two resident species: the Northern Waterthrush occurs in the lowlands and the Louisiana Waterthrush mainly at midlevels and in the mountains; and the resident Yellow Warbler in the lowlands and the resident Arrow-headed Warbler at midlevels and in the mountains. A few other parulids — the Parula and Prairie Warblers and American Redstart — are much commoner in lowland than montane forest. The subdivision of the main types of lowland forest in Table 5 again shows no species separated by habitat though some are more common in the wetter, richer forests and others in the more arid types of lowland forest. This is due to their preference for feeding in trees with particular types of leaves. We classified differences of this sort as contrasts in feeding stations, not habitat.

## *Annotated List*

We first consider four specialized species, each of which has an obviously different ecological niche from any other, then five ground-feeding species, and finally 11 leaf-gleaning species that obtain most of their food off leaves by reaching from a perch. Only in the last group is there any difficulty in understanding how the various species might be separated ecologically from each other. The North American range and habitat are from Chapman (1917), Bent (1953), and Robbins *et al.* (1966); Tables 3 and 4 summarize the habitats in Jamaica; Tables 6 through 10 give the feeding stations and feeding methods. The totals differ somewhat in different tables partly because, at first, we did not always obtain pertinent information on the feeding.

## Four Specialists

Black-and-white Warbler (*Mniotilta varia*): Breeds in most of North America, preferring open and secondary growth in broad-leafed deciduous woods. Common in Jamaica in all types of natural forest, both open and closed, from mangroves and the most arid lowland forest to the wettest and highest montane forest and also in cultivated forest, including introduced pines. It is the only species which feeds primarily by creeping up and along trunks, branches, and twigs of all sizes, taking insects off bark or probing for them in crevices, and, occasionally, by following termite trails or climbing damp rocks or vertical banks with short vegetation. Rarely, it takes an insect off a leaf or catches in the air one that it has disturbed.

Worm-eating Warbler (*Helmitheros vermivorus*): Breeds in eastern United States on wooded hillsides with broad-leafed deciduous trees and saplings. Occurs in Jamaica in all types of natural forest, except mangroves, and in cultivated forest with rather thick cover. Generally, we found it low in trees but not on the ground. Although we did not see many, it was the fifth commonest species captured in our mist nets (Table 3), suggesting that

Figure 2. Midlevel wet limestone forest in a new clearing in the Cockpit Country, Jamaica.

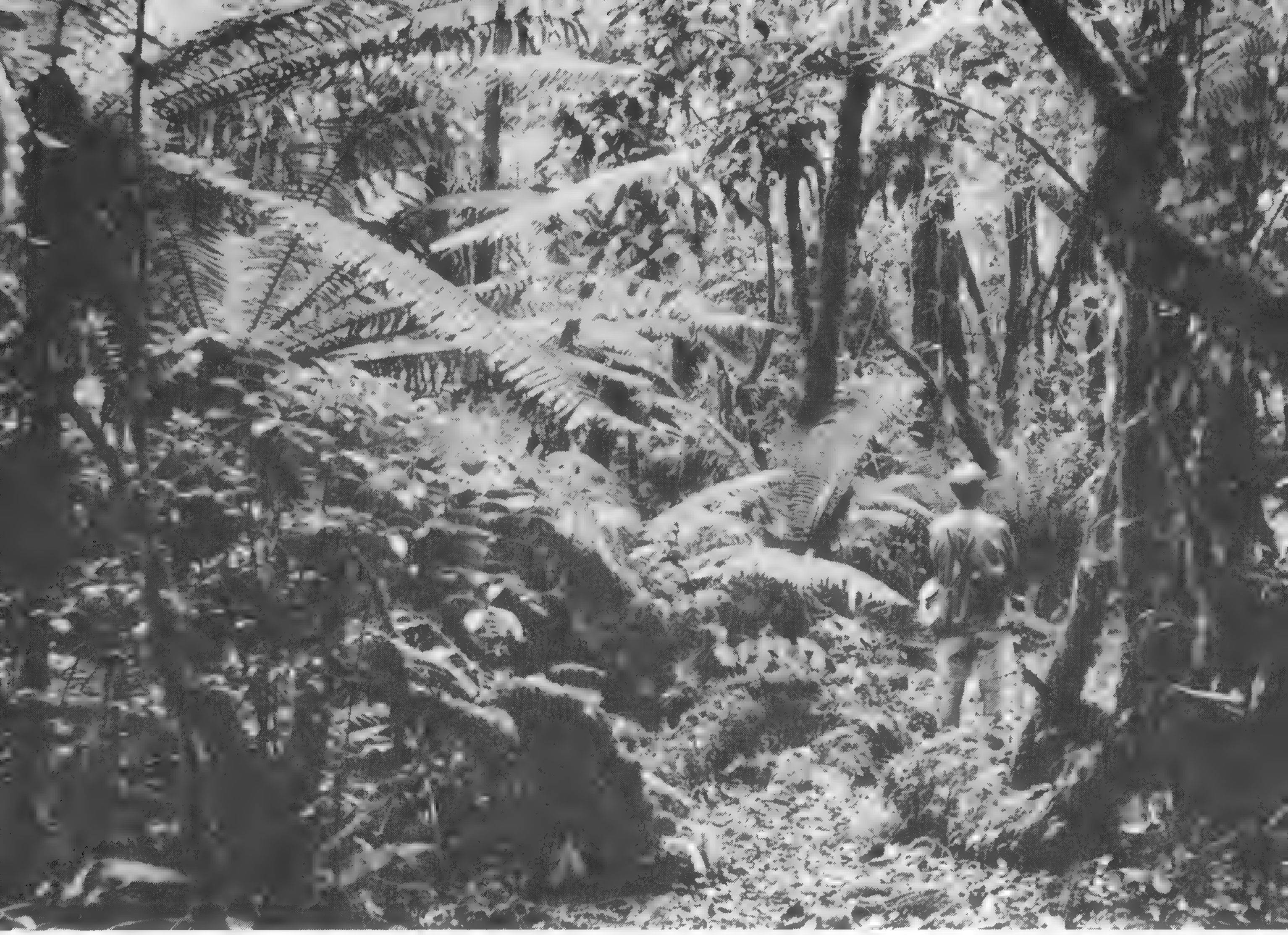


Figure 3. Montane cloud forest in the Blue Mountains, Jamaica.

it keeps low. It is the only warbler in Jamaica which feeds primarily by probing among clusters of hanging dead leaves or pulling bark from dead twigs. Often it feeds in the only cluster of dead leaves among many green ones.

Common Yellowthroat (*Geothlypis trichas*): Widespread in North America in tangled low vegetation at the edges of woods and swamps. Common in Jamaica in the lush herb layer, usually between 1.0 and 1.5 meters high, at the edges of swamps and some forests including montane forest. In the lowlands, it occurs at times in damp woodland, where there is no lush herb layer, and feeds up to 10 meters above the ground in thick bushes or low trees. It is the only warbler in Jamaica that feeds in thick herbage.

American Redstart (*Setophaga ruticilla*): Widespread in North America in broad-leafed deciduous forests with a rich understory. Found in Jamaica in all types of natural woodland, particularly mangroves, sea-level forest, and lowland riverine forest; scarce in the mountains. It is the only warbler in Jamaica which catches almost all of its prey in the air; the Magnolia Warbler feeds in this way some of the time and other species do so occasionally. Flashing its tail and darting out to take insects at any height — often just under the canopy, sometimes lower, and even on the ground — it takes quick, short flights never far from the vegetation where it hops among the twigs, especially the leafy twigs.

## TABLE 4

Number of Warblers Seen per Ten Hours of Slow Walking in Jamaica

| | *Natural forest* | | | | *Gardens, parkland* | | |
|---|---|---|---|---|---|---|---|
| *Species* | *Mangroves** | *Lowland* | *Mid-level* | *Montane* | *Lowland* | *Mid-level* | *Montane* |
| *Resident* | | | | | | | |
| Yellow | 62 | 1 | — | — | — | — | — |
| Arrow-headed | — | 2 | 11 | 18 | — | 5 | 10 |
| *Wintering* | | | | | | | |
| Black-and-white | 24 | 22 | 12 | 12 | 16 | 13 | 10 |
| Swainson's | — | 2 | x** | 2 | — | — | — |
| Worm-eating | — | 2 | 2 | 1 | 1 | 4 | 1 |
| Tennessee | — | 1 | — | 1 | 1 | — | 1 |
| Parula | 3 | 17 | 5 | x | 10 | — | 1 |
| Magnolia | — | 5 | x | x | 5 | 3 | x† |
| Cape May | — | 5 | — | — | 16 | 1 | 4 |
| Black-throated Blue | — | 10 | 13 | 6 | 4 | 25 | 14 |
| Myrtle | — | x | — | x | 7 | — | x |
| Black-throated Green | — | 3 | 2 | 1 | 3 | — | 7 |
| Yellow-throated | — | — | — | — | 2 | — | 3 |
| Prairie | 5 | 19 | 4 | x | 4 | 10 | 3 |
| Palm | 5 | 3 | x | x | 3 | 3 | 1 |
| Ovenbird | 6 | 7 | 2 | 2 | 3 | 3 | 2 |
| Northern Waterthrush | 35 | 2 | — | — | 5 | x | — |
| Louisiana Waterthrush | — | x | — | 1 | x | 10 | x |
| Common Yellowthroat | 6 | 14 | 3 | 3 | 7 | 15 | 3 |
| American Redstart | 29 | 17 | 7 | 1 | 3 | 28 | 1 |
| Total warblers | 174 | 131 | 61 | 49 | 90 | 121 | 60 |
| Total passerines | 230 | 396 | 392 | 180 | 676 | 401 | 319 |
| Number of hours | 9 | 86 | 30 | 65 | 10 | 8 | 40 |

*Mangroves censused much less often than other natural forests.

**x means recorded, but less than 0.5 birds per 10 hours.

†Seen in habitat, but only outside counts.

## TABLE 5

Number of Warblers Seen per Ten Hours in Lowland Dry Limestone Forest in Jamaica

| *Species* | *Forest type* | | | | | |
|---|---|---|---|---|---|---|
| | *Sea-level** | *Arid** natural* | *Arid*** cut-over* | *Typical† cut-over* | *Good†† secondary* | *Riverine‡* |
| *Resident* | | | | | | |
| Yellow | 8 | — | 2 | — | — | — |
| Arrow-headed | — | — | — | — | 8 | — |
| *Wintering* | | | | | | |
| Black-and-white | 22 | 14 | 3 | 25 | 16 | 35 |
| Swainson's | 3 | — | — | 3 | 1 | 2 |
| Worm-eating | 5 | 1 | — | 2 | 3 | 1 |
| Tennessee | — | — | — | — | — | 3 |
| Parula | 19 | 4 | 1 | 19 | 22 | 22 |
| Magnolia | 6 | — | — | 9 | 4 | 9 |
| Cape May | 6 | 1 | — | 10 | 4 | 4 |
| Black-throated Blue | 19 | 1 | — | 2 | 17 | 14 |
| Myrtle | — | — | — | 1 | — | — |
| Black-throated Green | — | 1 | — | 9 | 2 | 5 |
| Prairie | 29 | 11 | 4 | 30 | 7 | 22 |
| Palm | 3 | — | 1 | 12 | — | 1 |
| Ovenbird | 2 | 9 | 2 | 12 | 4 | 6 |
| Northern Waterthrush | — | — | — | 2 | — | 8 |
| Common Yellowthroat | 27 | — | 2 | 19 | 2 | 31 |
| American Redstart | 29 | 6 | — | 9 | 14 | 30 |
| Total warblers | 179 | 49 | 16 | 163 | 103 | 196 |
| Total passerines | 552 | 234 | 264 | 389 | 300 | 599 |
| Number of hours | 11 | 20 | 21 | 17 | 20 | 18 |

*Morant Point and Negril: parts liable to flooding, parts cut over.

**Hellshire Hills and Portland.

***Port Henderson Hill in Hellshires.

†Long Mountain beside University campus at Mona: much cut over.

††Valley up from Ferry (Fresh) River.

‡Along Ferry River and in woods beside Mona Reservoir.

## Ground-feeding Species (Table 8)

Swainson's Warbler (*Limnothlypis swainsonii*): Breeds in southeastern North America, mainly in flood-plain forest with thick undergrowth and also in forested mountain ravines. Commoner everywhere in Jamaica than our slow-walk counts suggest (Tables 2 and 3). Its apparent scarcity in the mid-level forest is probably due to our censusing at the forest edges, disturbing the bird, and causing it to fly into thick bushes before we saw it. It always feeds on the forest floor where it rummages and probes in leaf litter, sometimes tossing leaves aside just as it does in North America (Meanley, 1966). The only other parulid feeding on the forest floor in Jamaica is the Ovenbird, which picks up insects in its much shorter beak but does not probe.

Palm Warbler (*Dendroica palmarum*): Breeds in central and eastern Canada in swamps and bogs. Occurs in Jamaica mainly in the man-modified habitat of grassland with scattered trees and at the forest edge, chiefly in the lowlands though we saw one on the grassy top of Blue Mountain Peak. It is the only warbler in Jamaica which feeds primarily on grassy ground in the open. Occasionally, it snatches an insect from the vegetation or in the air, but the high number of such records in Table 7 is misleading because we failed to record all the normal feedings that we observed on the ground.

Ovenbird (*Seiurus aurocapillus*): Breeds in the eastern half of North America, mainly in broad-leafed forests with thick undergrowth. Common in Jamaica on the floor in all types of natural forest from the lowlands to the mountains, but uncommon in cultivated woods because it prefers thick tree cover. In the lowlands, we found the Ovenbird on dry ground and the Northern Waterthrush on muddy ground; in the wet, montane forest, we found the Ovenbird throughout but no Northern Waterthrushes. The Ovenbird picks insects off the leaf litter on the ground, usually under trees but also, unlike the Swainson's Warbler, on the forest paths and trails.

Northern Waterthrush (*Seiurus noveboracensis*): Breeds across Canada and northern conterminous United States, near standing water in forests and bogs. Abundant in Jamaica in mangroves. It is a regular, but sparse, inhabitant in lowland woods and cultivated woods on muddy ground, especially near standing water or muddy streams. We recorded it as high as 240 meters on trails through cultivated woods in the very wet limestone forest of the John Crow Mountains. It picks small invertebrates off mud or extremely shallow water. In the Kingston Botanic Garden, it walks on, and finds food on, the large leaves of an introduced water lily (*Victoria regia*).

Louisiana Waterthrush (*Seiurus motacilla*): Breeds in east-central United States, mainly south of the range of the Northern Waterthrush, usually beside rocky streams, but also in swamps. Occurs in Jamaica regularly in rather small numbers along rocky forest streams and, at times, along wider rocky rivers, chiefly at middle elevations and in the mountains, but also in the lowlands. It is the only warbler which feeds primarily from rocks beside or in the water. In the lowlands, it limits its feeding to rocks beside or in water, but at 500 meters elevation, near the Hermitage Reservoir where the Northern Waterthrush is absent, the Louisiana Waterthrush hunts regularly on mud and beside very shallow standing water — like the Northern Waterthrush in the lowlands. One individual fed again and again on a wet tarmac road through montane forest, and another on the stonework beside a pond in the Kingston Botanic Garden.

### Summary of Ground-feeders

Four of the five ground-feeding species hunt on different substrates, and the Swainson's Warbler and Ovenbird that share the forest floor feed differently. The Swainson's Warbler probes and the Ovenbird pecks (Table 8). In a lowland wood we once saw a Louisiana Waterthrush on a rock in midstream, a Northern Waterthrush two meters away at the muddy edge of the stream, and an Ovenbird six meters away on dry ground under trees. Since all three were on the ground in the same lowland wood, it is hard to decide whether they differed in habitat or choice of feeding station.

In Trinidad, 1,600 km southeast of Jamaica, where the Northern Waterthrush is the only species of *Seiurus* present, David Lack found it not only on mud in the mangroves, as in Jamaica, but also on the dry forest floor in the lowlands, like the Ovenbird in Jamaica. Mr. A. Lill (pers. commun.) also found it regularly beside rocky streams in the mountains, like the Louisiana Waterthrush in Jamaica.

TABLE 6

Food of Warblers in Jamaica*

| *Species* | *Number of feedings seen* | *Percentage of major food types* | | |
|---|---|---|---|---|
| | | *Insect* | *Fruit* | *Nectar* |
| *Resident* | | | | |
| Yellow | 67 | 100 | — | — |
| Arrow-headed | 392 | 96 | 3 | 1 |
| *Wintering* | | | | |
| Black-and-white** | 256 | 96 | 4 | — |
| Swainson's | 32 | 100 | — | — |
| Worm-eating | 60 | 100 | — | — |
| Parula | 503 | 92 | 6 | 2 |
| Magnolia | 177 | 100 | — | — |
| Cape May | 277 | 71 | 14 | 15† |
| Black-throated Blue | 372 | 94 | 2 | 4 |
| Black-throated Green | 374 | 95 | 5 | — |
| Yellow-throated | 61 | 100 | — | — |
| Prairie | 312 | 98 | 2 | — |
| Palm** | 81 | 100 | — | — |
| Ovenbird** | 106 | 100 | — | — |
| Northern Waterthrush** | 55 | 100 | — | — |
| Louisiana Waterthrush** | 45 | 100 | — | — |
| Common Yellowthroat | 97 | 99 | 1 | — |
| American Redstart | 322 | 100 | — | — |

*From mid-October to 15 April; resident species included for comparison.

**Observations include searchings as well as feedings; observations for other species include only actual feedings.

†Includes individuals taking sap from holes drilled by Yellow-bellied Sapsucker.

### Resident Leaf-gleaning Species

(Tables 6, 7, 9, 10, and 11)

Yellow Warbler (*Dendroica petechia*): Resident in Jamaica; almost confined in winter to the mangroves and woodland close to shore; occurs sparsely in the immediately adjoining forest. In April, when the wintering warblers leave, it broadens its habitats by moving into marsh forest and riverine woodland, including that along the Black, Ferry, and Sweet Rivers, up to at least eight kilometers from the sea. It is the only common leaf-gleaning warbler in the mangroves. Since we concentrated on other warblers in the mangroves and tended to record only the unusual feedings of the Yellow Warbler, the percentages of feedings from the air and on the ground, in Table 7, are misleadingly high.

Arrow-headed Warbler (*Dendroica pharetra*): Resident and endemic in Jamaica; breeds commonly in montane forest and regularly in mid-elevation forest. Many stay in mountains in winter; but there is an increase in numbers in the mid-elevation forest and rich lowland forest, as in Fern Gully and above the Ferry River where we saw one or two at 100 meters elevation in summer but did not find a nest. The Arrow-headed Warbler feeds primarily on insects from the fairly thick evergreen leaves of forest trees, usually fairly high above the ground, both in the canopy and below it; at times, it feeds off twigs, branches, or tree ferns. The montane habitat of the Arrow-headed Warbler separates it from all wintering warblers except, in part, the Black-throated Blue, which is also common in some types of lowland forest (Tables 4 and 5). The Arrow-headed Warbler uses a different niche in that it takes almost all its food from leaves, typically spending much more time on one twig, peering about, and stretching farther from its perch to take an insect than does the Black-throated Blue Warbler, which gathers over half its food from twigs, ground, or air (Table 7), and tends to feed lower in the trees (Table 10), to change its perch much more often, and to move faster through the trees.

### Wintering Leaf-gleaning Species

(Tables 6, 7, 9, 10, and 11)

Tennessee Warbler (*Vermivora peregrina*): Breeds across Canada in spruce and aspen forest. Occurs regularly in Jamaica in very small numbers in both lowland secondary riverine woodland and montane forest; we found one in the Kingston Botanic Garden. It takes insects off both large and small leaves, but since we saw this species too infrequently for quantitative assessment, we have omitted it from the main tables. Its small numbers are too few to compete seriously with the other warblers.

Parula Warbler (*Parula americana*): Breeds in eastern North America, most commonly in the southeast, in broad-leafed forest, swamp forest, and on the edges of coniferous forest. In Jamaica, one of the two commonest leaf-gleaners in dry, limestone lowland forest; the other is the Prairie Warbler. Small numbers of both species inhabit mid-elevation forests and both occur rarely in the mountains where they are almost restricted to introduced trees. In the lowlands, we found the Parula Warbler most common in richer, damper woodland, all secondary at the present time, and the Prairie Warbler in both natural and cut-over arid forest. This partial difference in habitat is due to

## TABLE 7

### Feeding Sites of Warblers in Jamaica

| | | *Insect-feeding sites** | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Species* | *Number of feedings observed* | *Broad leaves* | *Conifer needles* | *Bromeliads* | *Air* | *Ground* | *Twigs* | *Flowers or fruit* |
| *Resident* | | | | | | | | |
| Yellow** | 67 | 76 | — | — | 9 | 7 | — | 7 |
| Arrow-headed | 377 | 92 | — | 3 | 3 | — | 3 | — |
| *Wintering* | | | | | | | | |
| Black-and-white† | 246 | 11 | 2 | 2 | 7 | 6 | 70 | 3 |
| Swainson's | 26 | 4 | — | — | — | 96 | — | — |
| Worm-eating†† | 60 | 69 | — | 3 | — | — | 20 | 8 |
| Parula | 461 | 87 | — | — | 2 | — | 7 | 5 |
| Magnolia | 178 | 73 | — | — | 11 | — | 11 | 6 |
| Cape May | 198 | 81 | — | 1 | 11 | — | 4 | 4 |
| Black-throated Blue | 350 | 46 | 2 | — | 17 | 15 | 13 | 8 |
| Black-throated Green | 354 | 61 | 26 | — | 5 | — | 6 | 3 |
| Yellow-throated | 61 | — | 72 | 8 | — | — | 11 | 8 |
| Prairie | 305 | 84 | 2 | — | 5 | 1 | 7 | 2 |
| Palm | 81 | 9 | — | — | 15 | 77 | — | — |
| Ovenbird | 106 | 1 | — | — | — | 94 | 5 | — |
| Northern Waterthrush | 55 | 2 | — | — | — | 98 | — | — |
| Louisiana Waterthrush | 53 | — | — | — | — | 100 | — | — |
| Common Yellowthroat | 96 | 65 | — | — | — | 11 | 19 | 5 |
| American Redstart | 322 | 28 | — | — | 64 | x | 8 | — |

*Figures indicate percentages of insects taken at given site.

**Five "ground feedings" were actually from the surface of water.

†Of 27 feedings on broad leaves, 70 per cent were on living leaves and 30 per cent on dead leaves.

††Of 60 feedings, 75 per cent were on dead leaves, 18 per cent on living vegetation, and 7 per cent not recorded.

the tendency of the Parula to feed in trees with broad thin leaves and the Prairie to feed in mimosaceous trees and others with very small leaves. No doubt the two species are separated in their feeding, but we discovered the difference in their choice of leaves too late for quantitative records of the critical points. In addition to the preference for different leaf types, the Parula prefers taller and denser trees and usually feeds in the upper levels, at times near the trunk and on creepers, moving rather slowly through the vegetation. It rarely feeds in flight. The Prairie Warbler moves rapidly through low, scrubby and rather open trees, typically feeding among the leaves at the ends

TABLE 8

Feeding Sites of Ground-feeding Warblers in Jamaica*

| *Species* | *Forest floor* | *Ground at forest edge* | *Mud in shallow water or beside it* | *Rocks by water* | *Short grass and trees* | *Any ground* | *Herbage* | *Air* |
|---|---|---|---|---|---|---|---|---|
| Swainson's | 77 | — | — | — | — | 20 | 4 | — |
| Palm | 2 | 11 | — | — | 48 | 15 | 9 | 15 |
| Ovenbird | 30 | 20 | 2 | 5 | 8 | 28 | 7 | — |
| Northern Waterthrush | — | — | 89** | — | — | — | 2 | — |
| Louisiana Waterthrush | — | 9 | 38 | 53 | — | — | — | — |

*Figures indicate percentages of feedings observed at a given site.

**Nine per cent on leaves of water lily (*Victoria regia*) in Kingston Botanic Garden.

of branches and in the crowns of low open trees and, while it often feeds from a perch, it also picks many insects off leaves and branches while hovering. One other species, the Magnolia Warbler, prefers the same type of tree as the Parula. In North America, in summer, the Parula may feed more from the tips of branches, at least in conifers, than it does in Jamaica (Morse, 1967, 1971). On spring passage to North America, it frequents taller trees than the Prairie Warbler (Parnell, 1969).

Magnolia Warbler (*Dendroica magnolia*): Breeds in Canada and northeastern United States, primarily in spruce and hemlock forests, especially thickets. In Jamaica, rather scarce, encountered mostly in rich lowland forest, less frequently at mid-elevations and in the mountains where it is found almost always in and at the edges of introduced trees, and absent from the arid lowlands. In the lowland forest, we found the Magnolia Warbler feeding in trees with broad thin leaves, like the longer-billed Parula Warbler, but it prefers the lower half of somewhat taller trees, whereas the Parula Warbler forages in the upper half (Table 10). Furthermore, the Magnolia Warbler moves much more rapidly through the vegetation than the Parula Warbler and takes a higher percentage of its insects off twigs and from the air. In its aerial feeding, it resembles the American Redstart. In summer in Maine, the Magnolia likewise feeds lower in the trees than the Parula (Morse, 1967, 1971).

Cape May Warbler (*Dendroica tigrina*): Breeds in spruce and fir forests of Canada and northern conterminous United States, especially in park-like areas. In Jamaica, occurs mainly in parkland and at the edges of woodland. Although the data in Table 4 suggest that it occurs mainly in the lowlands, we saw it rather often outside the census areas in open woods and partly cultivated areas at mid-elevations and in the mountains. It usually feeds in the upper levels of deciduous, not coniferous, trees with small leaves, preferring much higher trees than the Prairie Warbler. The Cape May Warbler travels rather slowly through the trees and, unlike other warblers, may peck repeatedly — as many as 20 times — at the same leaf, suggesting that it takes extremely small, plentiful insects, such as aphids. Frequently, it takes insects in the air (Table 7) or from leaves by hovering (Table 9), and it eats more small fruits and nectar than the other parulids (Table 6), sucks sap from holes drilled in eucalyptus by the Yellow-bellied Sapsucker (*Sphyrapicus varius*), as in other kinds of trees in North America (Foster and Tate, 1966), and visits hummingbird feeders in gardens.

Myrtle Warbler (*Dendroica coronata*): Breeds in Canada and northern conterminous United States in spruce-fir forests. Arrives in Jamaica much later than the other species — we first saw it on 10 January — and although in some years it is a common transient, so few stay for the winter that we did not observe enough feeding to include it in the tables. We saw four Myrtle Warblers in mimosaceous trees in cultivated woodland near Kingston, two in introduced pines, and one in mountainous sclerophyllous forest — forest characterized by trees with small, narrow leaves. The preferred types of trees suggest potential competition with the Cape May or Black-throated Green Warblers, but the Myrtle Warbler is larger than either of them, and we did not see it feeding in the terminal twigs of the canopy or side branches, as they do, a difference that continues through the summer (MacArthur, 1958).

Black-throated Green Warbler (*Dendroica virens*): Breeds in coniferous and mixed forests in Canada and northern conterminous United States. In Jamaica, occurs regularly in woodland at all altitudes. We saw it most frequently in secondary woodland in the lowlands near Mona, and in junipers and introduced pines in the mountains, and sometimes also in natural montane forest where it usually foraged for fruits. In the lowlands, it usually feeds in small-leafed, mimosaceous trees. In this way, its niche resembles that of the Prairie Warbler, except that the Black-throated Green Warbler feeds to a greater extent in taller trees of this type, usually at the top or on the tips of the branches. More importantly, the Black-throated Green is almost absent from the lowland forest where the Prairie Warbler is common, and widespread in the mountains where the Prairie Warbler is absent. In the mountains, only the Black-throated Green feeds commonly among juniper needles and only one other leaf-gleaner, the Yellow-throated Warbler, is common in the introduced pines. While the Yellow-throated Warbler probes for food, the Black-throated Green picks insects off the needles, especially the needles at the tips of the canopy and side branches, usually when perched, but often when hovering. It does the same in summer (MacArthur, 1958; Morse, 1967).

Black-throated Blue Warbler (*Dendroica caerulescens*): Breeds in southeastern Canada and northeastern United States. In Jamaica, recorded commonly in rich lowland forest, mid-elevation and montane forest, and in cultivated woodland; absent from the arid lowland forest. It differs from the other leaf-gleaners in that it feeds much more often on the ground, in the air (Table 7), and off twigs. When feeding off leaves, it tends to be close to the ground (Table 10). Furthermore, it differs from all the other species, except the Arrow-headed Warbler, in preferring to feed in trees with broad, rather thick leaves.

Yellow-throated Warbler (*Dendroica dominica*): Breeds in southeastern North America in open pine woods and in broad-leafed trees covered with Spanish moss (*Tillandsia* sp.). In Jamaica, found regularly in small numbers in introduced pines in both lowlands and mountains; also occurs in the Kingston Botanic Garden. When foraging, it probes its relatively long bill into the bases of pine needles or the small narrow leaves of the xerophytic species of *Tillandsia*. Ficken *et al.* (1968) and Morse (1968) described its summer feeding habits.

Prairie Warbler (*Dendroica discolor*): Breeds in eastern North America in scrubby, broad-leafed and coniferous forests and at the forest edge. In Jamaica, the commonest leaf-gleaner in all types of lowland forest except good secondary forest; occurs especially in the more open areas and places where scrubby mimosaceous trees predominate. It is sparse at mid-elevations and rare in the mountains where we found it only at the forest edge and in cultivated woodland. It takes insects off leaves at the ends of side branches and in the canopy, usually from a perch, but often by hovering. Its preference for low mimosaceous trees separates it from most other species. We described the ways in which it differs from the Parula, Cape May, and Black-throated Green Warblers in the discussions of those species.

### Summary of Leaf-gleaners

Table 11 indicates the probable ways by which the nine common leaf-gleaners are isolated ecologically from each other. The two resident species,

TABLE 9

Behavior of Warblers Feeding on Insects in Trees or Herbage in Jamaica

| *Species* | *Activity of bird** <br> *Perched* | <br> *Flying* | <br> *Hovering* | <br> *Fluttering from perch* | *Total*** *of insects feedings* |
|---|---|---|---|---|---|
| *Resident* | | | | | |
| Yellow | 81 | 16 | 3 | — | 67 |
| Arrow-headed | 96 | 3 | x† | — | 377 |
| *Wintering* | | | | | |
| Black-and-white | 93 | 6 | 1 | x | 246 |
| Worm-eating | 100 | — | — | — | 60 |
| Parula | 95 | 3 | 2 | x | 461 |
| Magnolia | 79 | 12 | 6 | 3 | 178 |
| Cape May | 75 | 11 | 14 | — | 198 |
| Black-throated Blue | 72 | 18 | 8 | 2 | 350 |
| Black-throated Green | 78 | 5 | 14 | 3 | 354 |
| Yellow-throated | 98 | — | 2 | — | 61 |
| Prairie | 82 | 5 | 11 | 2 | 305 |
| Common Yellowthroat | 99 | 1 | — | — | 96 |
| American Redstart | 15 | 81 | 3 | 1 | 322 |

*Figures indicate percentages of insects captured by each method.

**From Table 7.

†x indicates less than one per cent.

## TABLE 10

### Height at Which Leaf-gleaning Warblers Feed in Jamaica

| *Species* | *Feedings at all heights* | | | *Feedings at three meters and higher* | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | *Percentage in* | | | |
| | *Number of* observations* | *Mean** height* | *Standard** deviation* | *Number of* observations* | *Lowest quarter* | *Second quarter* | *Third quarter* | *Top quarter* |
| *Resident* | | | | | | | | |
| Yellow | 17 | 5.6 | 4.5 | 13 | 0 | 31 | 23 | 46 |
| Arrow-headed | 107 | 6.8 | 4.1 | 76 | 4 | 28 | 30 | 38 |
| *Wintering* | | | | | | | | |
| Parula | 131 | 6.4 | 3.6 | 105 | 4 | 28 | 31 | 38 |
| Magnolia | 49 | 6.3 | 3.3 | 46 | 7 | 50 | 22 | 22 |
| Cape May | 39 | 7.6 | 3.5 | 38 | 0 | 18 | 34 | 48 |
| Black-throated Blue | 152 | 4.5 | 4.0 | 67 | 6 | 36 | 30 | 28 |
| Black-throated Green | 81 | 7.8 | 4.0 | 72 | 1 | 24 | 32 | 43 |
| Yellow-throated | 11 | 8.6 | 4.7 | 11 | 0 | 36 | 36 | 27 |
| Prairie | 93 | 5.3 | 4.0 | 59 | 3 | 34 | 21 | 42 |

*Each observation represents a different bird.

**Meters.

the Arrow-headed and Yellow Warblers, maintain their separation through their preference for different habitats. The wintering species differ markedly from each other in the type of leaves preferred for feeding, their feeding stations, or feeding methods. These differences might well suffice for full ecological isolation although more detailed study is necessary. We may add that no ecological separation was obvious to us when we first observed this diversity of similar-sized species in the Jamaican forests in October 1970.

## *Discussion*

### Comparison of Summer and Winter Ecology

Of the 18 species of parulid warblers wintering in Jamaica, four — the Black-and-white Warbler, Ovenbird, Common Yellowthroat, and American Redstart — occur widely in summer in eastern North America from Canada to the southern United States. The summer range of a fifth, the Parula Warbler, overlaps these four except in the north. Seven others — the Tennessee, Magnolia, Cape May, Myrtle, Black-throated Green, and Palm Warblers and the Northern Waterthrush — breed mainly in the coniferous forests of Canada and northeastern United States. The Black-throated Blue Warbler

## TABLE 11

### Major Mechanisms of Ecological Separation in Leaf-gleaning Warblers in Jamaica

| | Yellow | Arrow-headed | Parula | Magnolia | Cape May | Black-throated Blue | Black-throated Green | Yellow-throated |
|---|---|---|---|---|---|---|---|---|
| Arrow-headed | H | | | | | | | |
| Parula | H | H | | | | | | |
| Magnolia | H | H | PS | | | | | |
| Cape May | H | H | LPS | LSN | | | | |
| Black-throated Blue | H | (H)S | (H)LS | (H)LS | LSN | | | |
| Black-throated Green | H | (H)L | LPS | LPS | LSN | LPS | | |
| Yellow-throated | H | H | HLP | LS | LSN | LPS | LS(N) | |
| Prairie | H | H | LP | LS | HSN | (H)LPS | H(P)? | HL |

The symbols indicate the following means of separation:

H By habitat: mangroves, lowland dry forest, mid-elevation forest, montane forest, or parkland.

L By leaf-type feeding: mainly on narrow mimosaceous leaves, broad thin leaves, pine needles, or juniper needles.

P By feeding on given part of tree: mainly in upper or lower section, near trunk, or on terminal twigs.

S By feeding station on insects: off leaves from perch, in the air, from twigs, on the ground, or for those in conifers whether or not taken from base of needles by probing.

N By type of food besides insects, mainly fruit or nectar.

A single H indicates clear-cut separation by habitat even though there may be other important differences in feeding.

An H, followed by another letter, indicates partial separation by habitat and the rest by other factors.

A letter in parentheses means that that particular difference is of less importance.

Tennessee and Myrtle Warblers omitted because of scarcity; Myrtle separated from others mainly by size and somewhat by feeding station.

breeds farther south and not as far north as these seven, and lives in broadleafed forest instead of coniferous forest. The remaining five — the Swainson's, Worm-eating, Yellow-throated, and Prairie Warblers and the Louisiana Waterthrush — breed in eastern North America, except in the extreme northeast, and hardly come in contact with the seven northern species until they meet in Jamaica during the winter.

The ecology of at least most of these species is similar in Jamaica in winter to that in North America in summer. This is true with respect to habitat, for instance, in the Northern and Louisiana Waterthrushes and Common Yellowthroat. The Black-throated Blue prefers broad and rather thick-leafed trees in Jamaica and nests in heavy broad-leafed forest. The Black-throated Green and Yellow-throated Warblers often frequent conifers in both regions. However, some others, including the Tennessee, Magnolia, and Cape May Warblers, which breed in conifers, do not normally frequent conifers in Jamaica. The feeding methods are similar for the Black-and-white and Swainson's Warblers, Ovenbird, and American Redstart in Jamaica and North America. A comparison with the studies of MacArthur (1958) and Morse (1967) shows that the Magnolia, Cape May, Myrtle, and Black-throated Green Warblers feed in the same sites and in the same ways in Jamaica and North America. For various other species we have no published quantitative observations, but the general descriptions are consistent with what we found in Jamaica, except possibly in the Parula and Yellow-throated Warblers (Morse, 1967, 1968; Ficken *et al.*, 1968).

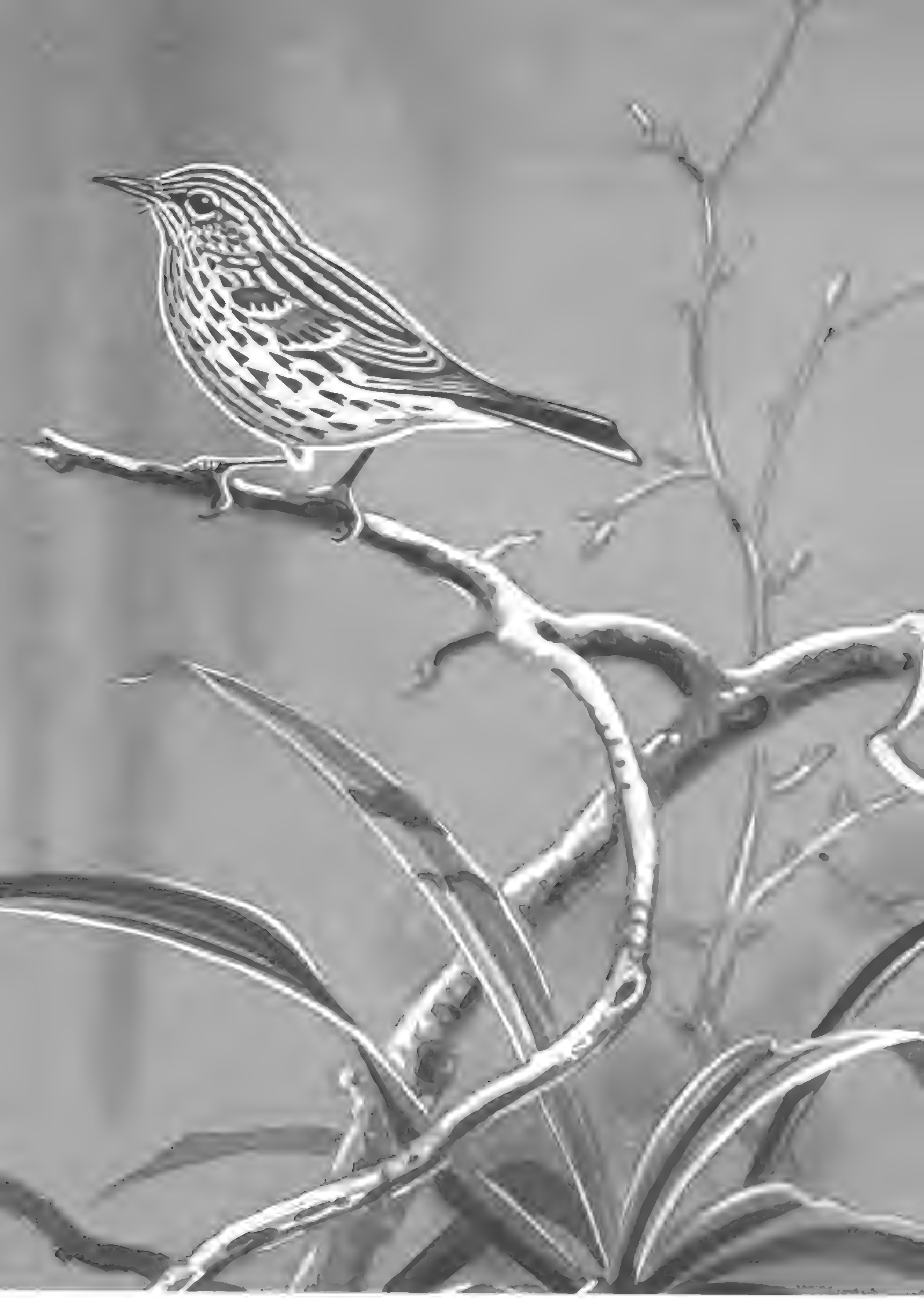
## Evolution of Ecological Isolation

At least most of the warblers in Jamaica appear to be isolated ecologically from each other (Tables 8 and 11).

The little evidence so far available (reviewed in Lack, 1971) suggests that a young passerine finds the habitat of its species partly through innate factors and partly through experience — what it sees when recently fledged and in the company of its parents. In contrast, the specific feeding stations and feeding methods seem mainly to be acquired through experience, the young passerine gradually discovering for itself which methods are the most rewarding, although it may also learn by watching others of its kind. The main factors responsible for success or failure in feeding are the bird's morphological, or physical, adaptations in bill, leg, musculature, and so on. This explains why species of the same genus that live in the same habitat often differ greatly in size of bill. Otherwise, they might seriously compete with each other for food. *Dendroica* warblers seem exceptional, both in the large number of coexisting species and in the small differences in the morphology of the different species. Nevertheless, differences exist and, though slight, might well be sufficient to promote ecological isolation.

A species that shares its mainland range with a congener may, on an island where the congener is absent, expand its ecological niche. Under these circumstances in the Southwest Pacific, frequent expansions occur in type of habitat, altitudinal zone, or a vertical feeding zone within a forest, but an expansion in foraging techniques or diet is rare without a marked morphological change in the island form concerned (Diamond, 1970).

The fact that at least 19 of the 20 wood warblers in Jamaica in winter differ in important ways from each other in ecology cannot be due to chance, and, presumably, means that competitive exclusion operates in the winter



Arrow-headed Warbler, *Dendroica pharetra*. Painting by John Henry Dick.

quarters. Jamaica, like other oceanic islands, has relatively few resident passerine species, and these few are characterized by relatively broad ecological niches. On the other hand, it has many wintering warblers with relatively narrow ecological niches, characteristic of passerines on continents. This contrast suggests that the warblers probably evolved the differences, on which their ecological isolation in Jamaica depends, on their continental breeding grounds. This view may need some modification since the wintering species from Canada do not meet those from southeastern United States when on the breeding ground. Furthermore, at least one species has modified its preferred habitat in the winter quarters. The Northern Waterthrush has a much broader habitat on Trinidad than in Jamaica.

In addition to the 18 regular wintering parulids, 12 North American warblers occur as transients in Jamaica: Prothonotary (*Protonotaria citrea*), Golden-winged (*Vermivora chrysoptera*), Blue-winged (*V. pinus*), Nashville (*V. ruficapilla*), Caerulean (*Dendroica cerulea*), Blackburnian (*D. fusca*), Chestnut-sided (*D. pensylvanica*), Bay-breasted (*D. castanea*), Blackpoll (*D. striata*), Pine (*D. pinus*), Kentucky (*Oporornis formosus*), and Hooded (*Wilsonia citrina*). Moreover, since there are few bird watchers in Jamaica, there may be still other species that occur there occasionally.

The transients would surely stay for the winter if they could live better there than elsewhere. Competition from the two resident species and 18 wintering species is probably the main reason for their moving on. Hence, even if the feeding adaptations of each species have evolved primarily in relation to the breeding grounds — which is not certain — these adaptations are critical in determining which of the warblers can survive the winter in Jamaica.

The nearest mainland to Jamaica is Honduras which, according to Monroe (1968), has about 242 breeding passerine species of which 14 are parulids; Jamaica has 35 breeding passerines with two parulids. Comparing Honduras and Jamaica, the number of breeding species in Jamaica is only 14 per cent of the number in Honduras; similarly, the number of breeding parulids in Jamaica is 14 per cent of the number in Honduras. Such figures are typical of the difference in numbers of species between a continental area and an oceanic island. In winter, the proportion changes: Honduras has 30 regular visiting parulids; Jamaica has 18 — 60 per cent of the number in Honduras. Of the 30 in Honduras, 13 are regular in winter in Jamaica and another six are transients. The Swainson's, Parula, Cape May, Black-throated Blue, and Prairie Warblers winter regularly in Jamaica but not in Honduras.

The traditional explanation for the small number of resident land birds on oceanic islands is the difficulty of dispersal from the mainland. We doubt this in general (Lack, 1969). Anyway, it does not hold for parulids in Jamaica. In addition to the two resident warblers, another 30 parulids have been recorded there, many of them regularly. What prevents at least some of these 30 from evolving breeding populations on Jamaica? That only two species breed on Jamaica conforms with the general proportion in numbers of terrestrial species compared to the nearest mainland; so whatever factors are responsible for fewer species breeding evidently operate on the warblers in summer. Why do these factors not operate in winter? Moreover, this high number of wintering species in Jamaica holds solely for parulids. Only two other North American passerines are regular in Jamaica in winter, the Catbird (*Dumetella carolinensis*), which is very sparse, and the Indigo Bunting (*Passerina cyanea*), which appears locally, mainly after 21 December. The only other wintering land bird, the Yellow-bellied Sapsucker, occurs widely on the island.

The problem of bird species diversity with respect to winter visitors deserves further attention, and the parulids, with numerous species, afford an excellent opportunity for studying the problem. In particular, we need figures for other islands. Fewer parulid species winter in Puerto Rico (C. B. Kepler and A. K. Kepler, pers. commun.) than in Jamaica, and still fewer winter in the Lesser Antilles. In Jamaica, only the Yellow Warbler breeds in the lowlands — in mangroves and littoral and riverine woodland. Great areas of arid and semi-arid limestone forest are untenanted. Surprisingly, no other species of warbler summers in the lowlands — unless we consider the Bananaquit (*Coereba flaveola*) a parulid. We cannot comment further on this point without knowledge of the seasonal variations in the numbers of insects available to the warblers.

## Foraging Parties

Insectivorous birds of diverse species characteristically form foraging parties in both tropical forest and north temperate woodland. Warblers join such parties in both winter and summer quarters (Eaton, 1953; Morse, 1970). In a typical party, the flock moves steadily through the forest, each individual keeping from one to a few meters from its nearest neighbors, maintaining contact by calls, and feeding in its specific fashion. In Jamaica, we observed no foraging parties.

Instead of foraging parties, we saw what we called "collections." When we stopped to observe a bird feeding, we often spotted an individual of another species a few meters away, though rarely as close as two meters. A collection might include up to five or six, rarely as many as eight, birds with not more than two of the same species, feeding in an area of perhaps 40 meters square. Both ground-feeding and arboreal parulids are frequently a part of such a collection, and they may associate with virtually any of the resident forest birds — other passerines, woodpeckers, or doves. A collection differs from a typical foraging party in that only a small number of individuals are involved, the individuals are more widely spaced, there are no regular contact calls, and the birds do not travel together through the forest. Instead, each stays near where first seen for several minutes and then gradually drifts away, seeming to be independent of the others.

At first, we thought we might be seeing apparent collections because, when we saw a bird, we usually stopped to watch it feeding, and perhaps we were seeing more birds in the forest when standing still than walking. However, on random stops in the forest, we often saw no birds, and saw no more standing still than walking. We ruled out the possibility that the collections might be the result of a purely random distribution since they were so definite and so frequent. At the same time, we should not exaggerate their frequency; we saw the species concerned singly more often than in collections. Most collections occurred where both parulids and resident birds were sparse, in very arid lowland forest and in montane forest; this was probably because we noticed such collections more readily where the birds were sparse. Where birds were more numerous, a group of a few widely spaced individuals did not attract our attention. We have, of course, excluded here the instances in which several birds fed at a common food source — a fruiting tree or a swarm of insects. In a collection, each bird feeds on its own, each species often in a different way from the rest; and while the collection includes mostly insectivorous birds, a seed-eater or fruit-eater sometimes joins the group.

Why are typical foraging parties absent from Jamaica? Such parties that include warblers occur on other islands of the Greater Antilles, including Cuba (Eaton, 1953), Hispaniola, and Puerto Rico (C. B. Kepler and A. K. Kepler, pers. commun.). The Jamaican forest has no avian predators on passerine birds; Cuba, Hispaniola, and Puerto Rico do have — accipitrine hawks. Although this fits with the theory that an advantage of feeding in mixed flocks is that several birds are more likely than one to notice an approaching predator (Lack, 1954), we are reluctant to believe that the absence of avian predators is the main factor responsible for the absence of foraging flocks in Jamaica.

## Summary

At least 19 of the 20 parulid warblers found in Jamaica in winter have marked ecological differences from each other: One climbs branches and twigs; one feeds from hanging dead leaves and twigs; one lives in thick herbage; and one flycatches. There are also five ground-feeders — four separated by the type of terrain; two, inhabitants of the same terrain, are separated by feeding method — one probes and the other picks. Of the 11 leaf-gleaners, the two resident species are separated largely by habitat; the rest mainly by feeding methods, the parts of the tree in which they feed, or the type of leaf from which they take insects.

In Jamaica, where the Northern Waterthrush, Louisiana Waterthrush, and Ovenbird occur, the Northern Waterthrush confines its activities to mud in the lowlands; in Trinidad, where the Louisiana Waterthrush and Ovenbird do not occur, the Northern Waterthrush broadens its habitat to include the edges of rocky streams and dry forest.

Various warblers frequent riverine forest in Jamaica in winter; when the visitors leave in April, Yellow Warblers move into the riverine forest to breed. No warblers breed in the lowland, dry limestone forest.

The number of breeding passerines on Jamaica is 14 per cent of that in Honduras; the proportion of breeding parulids is the same. The small number of parulids breeding in Jamaica is not due to the failure of other parulid species to reach the island. Another 30 species have been recorded there.

Eighteen warblers regularly winter in Jamaica, 60 per cent of the number wintering in Honduras. Another 12 warblers occurring in Jamaica as transients are presumably excluded by competition with the winter residents. We do not know why the factors responsible for the low species diversity and broad niches of resident land birds on oceanic islands, including Jamaica, do not operate just as intensely in winter as in summer.

We did not see foraging parties of insectivorous birds in Jamaica, but we did see parulids and resident forest species sometimes feeding near each other in loose "collections" of from two to eight individuals. Foraging parties occur in Cuba, Hispaniola, and Puerto Rico, and so do accipitrine hawks. There are no accipitrine hawks in Jamaica.

### *Acknowledgments*

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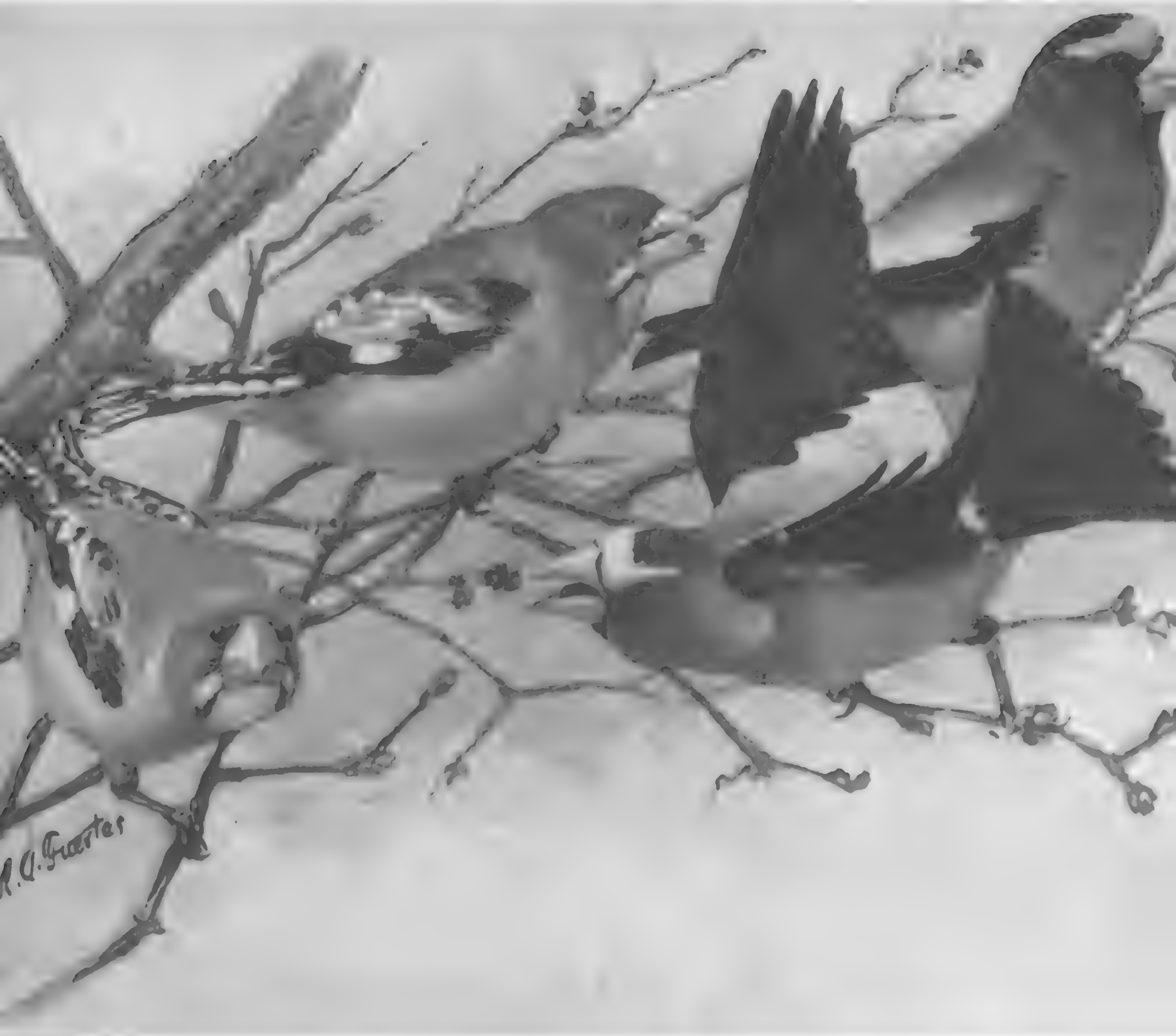


Evening Grosbeaks, *Hesperiphona vespertina.*
From a painting by Louis Agassiz Fuertes.

# THE DEVELOPMENT OF FOUR NORTH AMERICAN HERONS

William McVaugh, Jr.
Paintings by the author

The recent literature contains an abundance of information on the behavior and ecology of North American herons and egrets of the family Ardeidae, the results of several excellent studies. Yet, strangely enough, there is probably less information on the growth and development of the young of these species than almost any other. Treatises on the biology of birds tell very little; the "Handbook of North American Birds," Volume 1 (Yale University Press, New Haven, Connecticut, 1962), often simply states: "no details available on development of young" and "time span from hatching to independence not known." In an effort to help fill this hiatus, I have worked on four species — the Louisiana Heron *(Hydranassa tricolor)*, Black-crowned Night Heron (*Nycticorax nycticorax*), Common Egret (*Casmerodius albus*), and Little Blue Heron (*Florida caerulea*) — in the field, observing, measuring, and sketching. The following report is a summary of my results.

The detailed color plates show such characteristics as the sequence in growth patterns, the color changes in eyes, bill, tarsi, body skin, and the feather development. Illustrations depicting intraspecific color phases and interspecific growth relationships between nestlings of the same age have definite value and should be, according to G. M. Sutton (pers. commun.), ". . . extremely helpful to the taxonomists who must base their decisions on all that is known about the morphology and behavior of the form with which they deal."

## *Methods*

I collected my data for all four species from heronries on the Pea Island National Wildlife Refuge in North Carolina where I established a series of guidelines for gathering and evaluating my information, often working out my methods in the field by trial and error.

### Setting up the Study

To minimize the chaos that one often causes when approaching a heronry, I set up some exacting rules for entering the area and approaching these somewhat timid and diffident birds without causing them to abandon their nests. I knew full well that the more confusion I caused the longer it would take me to gather the data.

On my first trip to the heronry I realized that each of the four species reacted differently to my invasion and that I must spend hours, even days, just observing their habits. Thus, I selected an observation spot near, but outside, the heronry and moved it closer each day. The birds gradually became accustomed to my presence and I, after watching their flight patterns, nesting behavior, and other activities, determined the most suitable way and time to enter the rookery.

The color of my clothing apparently had little effect, but it did seem to be important that I wear the same clothes each time, thus establishing recognition by the herons. I entered the colony slowly, directly, and along the same path each time, retracing my steps when leaving. I never attempted to hide from the birds because I soon discovered that the sudden appearance of anyone invariably created panic. To lessen the chances of disturbing the adults bringing food to the nestlings or causing the nestlings to regurgitate their meal, I always visited the colony two or three hours after the early morning and late afternoon feedings.

Human entry into a heronry opens the way to predation from two major sources. Terrestrial predators following the scent into the colony may destroy eggs and young in nests close to the ground. I discouraged this by sprinkling naphthalene flakes along my trail. The common aerial predators, Common Crows (*Corvus brachyrhynchos*) and Boat-tailed Grackles (*Cassidix mexicanus*), are quick to take advantage of any disturbance in the colony that causes the adults to leave their otherwise guarded eggs and nestlings and, in the confusion, destroy both eggs and nestlings. One year, crows caused a 90-per-cent egg loss in the heron colony.

### Sample Size and Frequency of Visits

An acceptable sequence of development can be determined only by gathering a fairly large sample of information. My sample sizes were: Louisiana Heron, 65 nestlings; Black-crowned Night Heron, 36 nestlings; Common Egret, 21 nestlings; Little Blue Heron, 107 nestlings. I visited the colony every day to measure the birds and record the colors of the soft parts. Some individuals were checked every day; others every other day or every four to seven days, depending on the length of their nestling life.

### Aging

I believe it is possible to age a young heron, even if the hatching date is unknown, by using data compiled from the measurements of juvenal feathers. A nest containing more than one young shows a variable growth pattern reflecting not only the difference in hatching dates of the young, but also the keen competition for food with older and stronger nestlings often obtaining the lion's share. Even so, the growth of juvenal feathers seems to be constant in their development, showing a comparable growth in different young of the same age regardless of differences in body weight.

### Marking Nests and Handling Young

I identified each nest and its contents with a data tag enclosed in a plastic bag and fastened nearby. As the eggs hatched and the nestlings matured, I recorded additional information on the label. To establish its identity in the nest, I banded each nestling as soon as possible. The tarsus of a newly hatched nestling is usually too small to retain a band, so, until the foot was large enough, I found some identifying mark on each nestling to support the information I recorded.

I photographed, sketched, and recorded measurements and other data as quickly as possible. And different birds reacted in different ways to my handling; some were quiet and others aggressive, some calmed down quickly as I worked with them and others resisted.

## Kinds of Data Collected

I photographed and measured the nest and eggs for each species, and noted any unusual nesting condition. When eggs hatched, and periodically thereafter, I photographed young of known age, described the colors of the unfeathered, or soft, parts, and recorded linear measurements of bill, body, wing, secondary and primary feathers, tail, tarsus, and middle toe.

For one-day-old nestlings, I recorded minimum and maximum measurements. After the first day, the growth rate tended to vary more between nestlings of the same age, the variation depending upon the available food supply, the rate of parental feeding, and aggressiveness of the young.

In addition to recording colors, behavior, and measurements, I made sketches of the birds and, as the young developed, recorded an increasing number of topographic and physical features — from 29 to 67 — for each nestling. I banded each nestling with a U. S. Fish and Wildlife Service band for positive identification.

The color terminology, for the sake of simplicity, is based on the seven prismatic spectrum-color divisions and their intermediate values, plus black and white. I used other color terms, such as ivory, tawny, flesh, horn, and dusky, and described a body area with a singular or binomial color name — e.g., green or blue-green. Since any hue varies with intensity, I used modifiers such as pale, light, medium, and dark.

My statements on plumage are based on the average appearance and characteristics exhibited by a specific age group. I noted the emergence of the juvenal plumage and measured specific primaries and secondaries, the flight feathers of the wing, and rectrices, the flight feathers of the tail. When the young bird became more or less covered with feathers, I measured only the flight feathers in most cases. I described the color of the bare skin as long as it was visible.

## Measurements

For those interested in knowing how I made my measurements, I mention below my methods, which are largely those described in "Measurements of Birds" by S. P. Baldwin, H. C. Oberholser, and L. G. Worley (Sci. Publ. Cleveland Mus. Nat. Hist., 2:1–165, 1931).

Body length: from the tip of the bill to the tip of the longest rectrix with neck extended and the bird on its back.

Wing length (hand): from the distal bend of the wing, or wrist, marked by the junction of the forearm with the hand, to the tip of the hand excluding the feathers until the feathers emerge, at which time the length becomes the wing chord from the bend of the wing (wrist) to the tip of the longest primary.

Wing length (extended): measured across both extended wings from tip to tip.

Bill: the upper mandible from the base of the exposed culmen, the upper ridge, in a straight line to its tip.

Tail: the longest rectrix from its insertion in the follicle to its tip.

Tarsus: from the middle of the joint between the tibiotarsus and the tarsometatarsus behind to the lower edge of the lowest undivided scute on the front of the junction of the tarsometatarsus with the base of the middle toe.

Middle toe: from the junction of the middle toe with the foot to the distal end of the toe, excluding the claw.

## *Developmental Stages*

Descriptions and illustrations of the various developmental stages of four species of North American herons follow. For descriptions of color and size of eggs, I refer to A. C. Bent's "Life Histories of North American Marsh Birds" (U. S. Natl. Mus. Bull. 135, 1926) and C. A. Reed's "North American Birds Eggs" (Doubleday, Page and Company, New York, 1904). For anatomical terms, I followed "Ornithology in Laboratory and Field" by O. S. Pettingill, Jr. (Burgess Publishing Company, Minneapolis, 1970).

# LOUISIANA HERON

## *Egg Color*

The colors given by Bent (*op. cit.*) as "pale bluish green," "pale Niagara green," and "lichen green" do not agree with the basic color of approximately 175 eggs in 45 nests where the basic hue of all eggs was blue, not green, although a greenish cast was present. A more accurate description is pale greenish blue.

## *Age One Day*

### Plumage

"Tricolor" with long tawny down mixed with shorter gray down on the head; dark gray on the neck, back, and wings; and white down covering the under neck, abdominal region, and femoral tract.

### Unfeathered Parts

Exposed skin flesh-color under the neck, deep flesh or fleshy gray in the auricular region and nape of the neck, and bright blue to bluish gray around the eyes. Deep gray skin covers the crown and the remaining body skin varies in individuals from fleshy gray to medium gray.

Upper mandible fleshy gray to warm gray, black-tipped, a dark gray line on the cutting edge of the upper mandible only; pale pink inside nostril; egg-tooth present. Lower mandible flesh-colored with very small dark tip. Mouth lining yellow-pink to pink. Eye rather deep set in protruding dark gray eye-ring; iris light gray to off-white; pupil black. Tarsus and toes pale bluish pink on top and flesh-color below with varying intensity above; toe nails pale ivory and hallux toe nail darker.

### Measurements

Body length 101.6 to 107.9 mm; mean wing length 15.8 mm; bill length 12.7 to 15.8 mm; tarsus length 19.5 to 22.2 mm.

### Behavior

Just after hatching, while the down is still moist, the nestling may hold its head up and move the body in short, abrupt jerks. After the down dries in two to three hours and during the daylight observation periods, the young exhibits little or no reaction to humans.

## *Age Five Days*

### Plumage

Head covered with long, brownish red down, brownish gray down on the back, white down on the femoral tract, and white down sparsely covering abdominal area. Juvenal feathers emerging on humeral, femoral, and ventral tracts, including a narrow band on each side of neck; feathers on femoral and ventral tracts down-tipped.

### Unfeathered Parts

Exposed skin on ventral region of neck gray, fleshy gray on nape, pinkish gray under the chin, blue-gray to gray in orbital region, dark pinkish gray in humeral area, light pinkish gray on abdomen. Upper mandible dark gray proximally — almost black in some individuals — pinkish gray distally with dark tip; egg-tooth still visible; line on cutting edge of bill dark gray; inside nostril pink. Lower mandible dark gray proximally, pinkish gray distally with small dark tip; lower ridge, or gonys, dark gray. Mouth lining yellow-pink to pink. Iris light gray to off-white, pupil black, eye-ring dark gray. Tarsus and toes medium pinkish gray on top and grayish flesh underneath; nails light horn, ivory-tipped. Scales developing on tarsi and toes.

### Measurements

Body length 152.4 mm; wing length 31.8 mm; bill length 20.6 mm; tarsus length 28.6 mm; middle toe length 31.8 mm. Length of longest primary pinfeather 6.4 mm, longest secondary 4.8 mm, longest scapular 4.8 mm.

### Behavior

Capable of movement in nest, with nestlings interchanging positions; young are docile and easily handled, reacting slightly to movements of humans near the nest. They call repeatedly with a weak peeping note, but are quiet when handled. After being returned to the nest, they resume calling after five or ten minutes.

## *Age Eleven Days*

### Plumage

Head covered with long, light tawny down, sparsely mixed with dark gray down; some dark gray down on the back; white down on the femoral tract and abdominal area. Some juvenal feathers tipped with long white down; juvenal feathers emerging on capital tract, at base of bill, and under the neck on ventral tract.

### Unfeathered Parts

Exposed skin dark gray or pinkish gray under the neck; light pinkish gray on abdominal area. Upper mandible dark gray proximally, pinkish gray distally with dark tip; inside nostril reddish. Lower mandible dark gray proximally, pinkish distally. Mouth lining yellow-pink to pink. Iris off-white, pupil black, eye-ring medium gray. Tarsus and toes light gray, with pinkish gray on outside of tarsus, light gray underneath toes (varying in some individuals to pale green-gray); nails light horn, ivory-tipped. Scales well formed on tarsi and toes.

### Measurements

Body length 215.9 mm; wing 31.8 mm flattened; bill 30.2 mm; tarsus 39.7 mm; middle toe 55.6 mm. Length of primary pinfeather 22.2 mm; longest secondary pinfeather 22.2 mm; longest rectrix 9.5 mm; length of emergence from sheath of longest primary 3.2 mm; longest secondary emergence 15.9 mm; longest scapular emergence 12.7 mm.

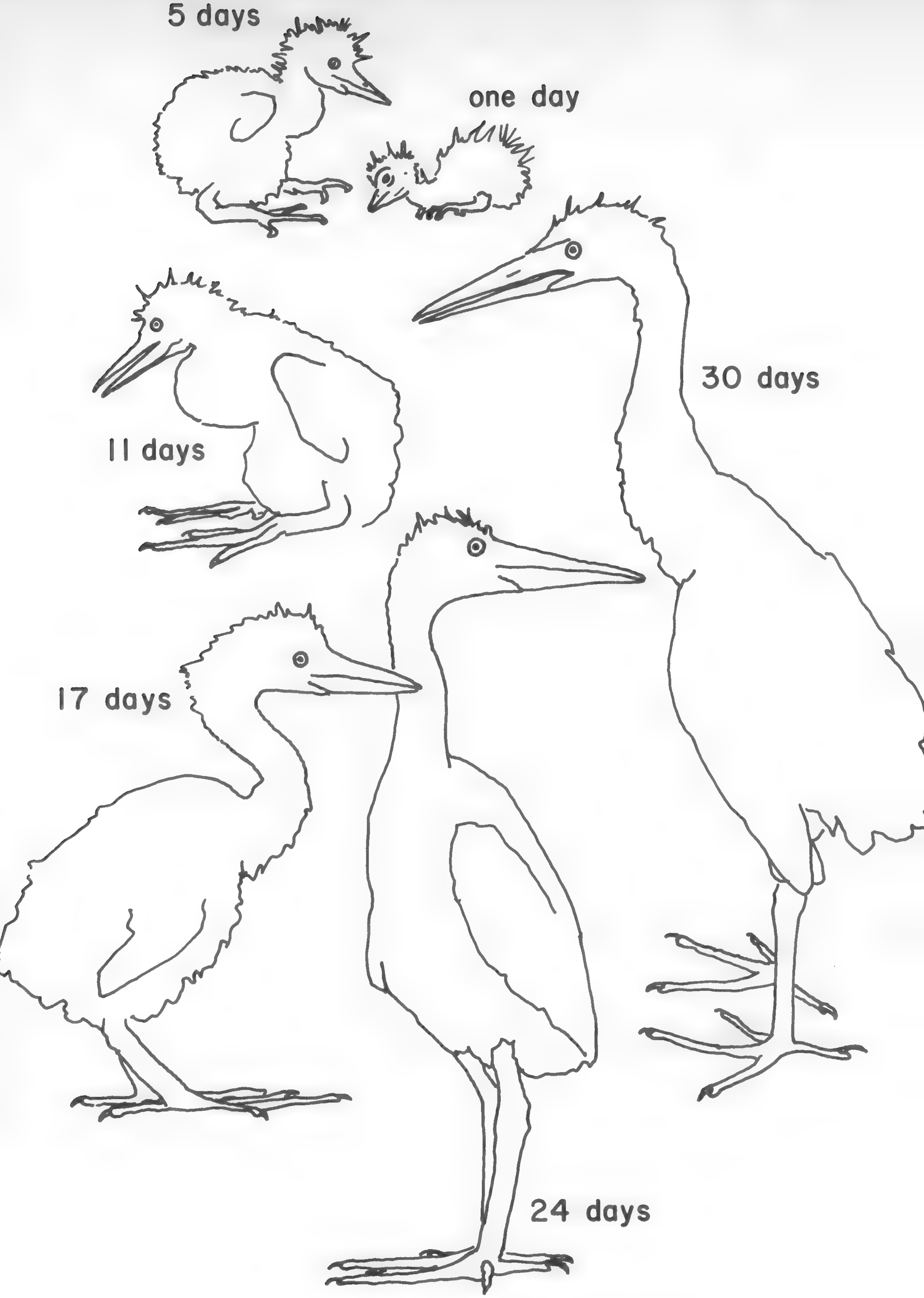
### Behavior

Young capable of climbing from the nest with bill, wings, and feet; sometimes perches above or to one side of the nest until parents approach with food; spends more time in than out of the nest; calls intermittently with a harsh note; shows fear when handled; when returned to the nest, usually climbs out immediately.

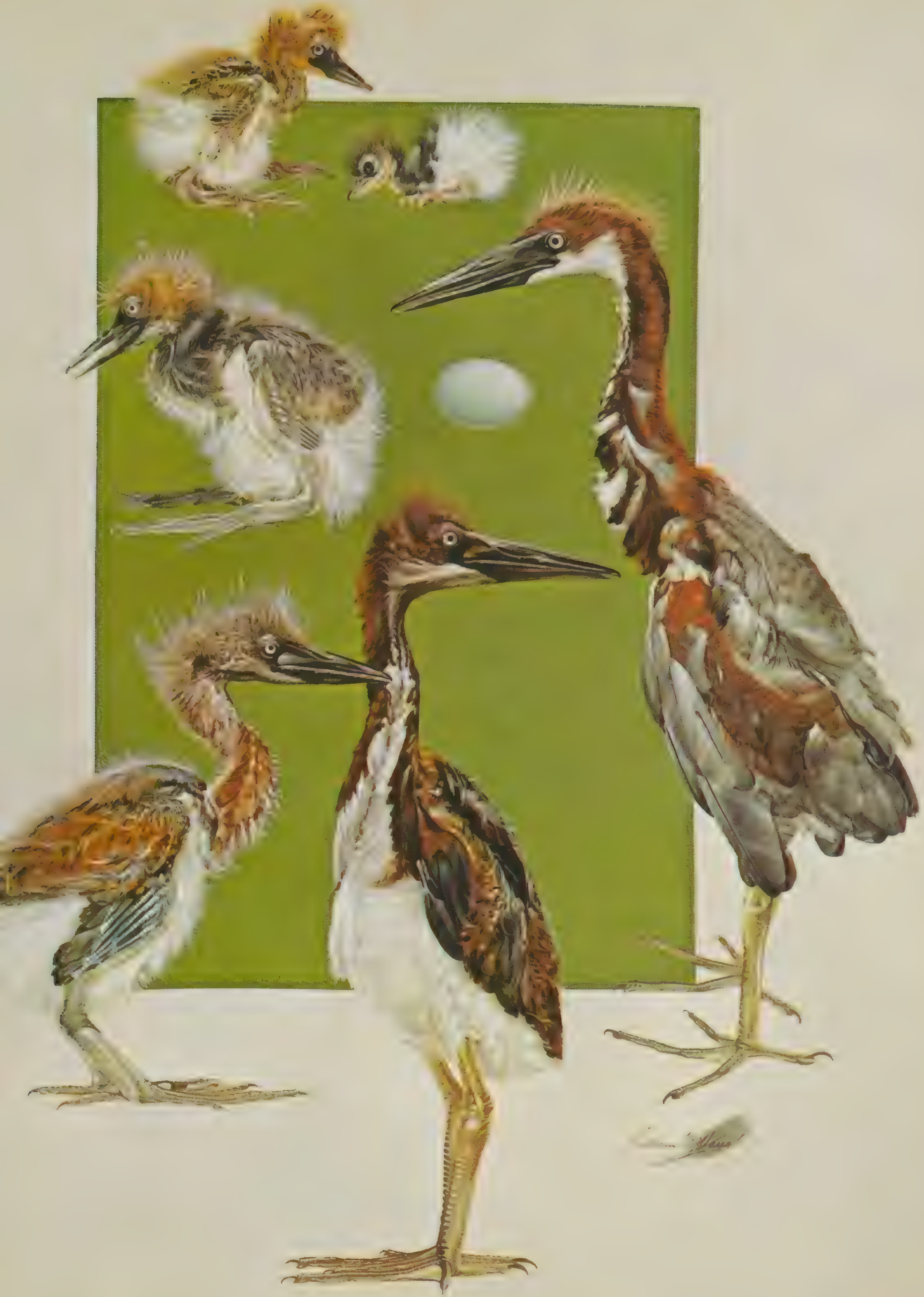
## *Age Seventeen Days*

### Plumage

Head covered with long, faded white down sparsely mixed with dark gray down; some dark gray down remaining on the back; reddish brown feathers just emerging from their sheaths on the upper half of the neck, lower half well emerged; white under-neck stripe becoming defined. Scapular and mantle feathers covering the upper back are mixed colors — some medium gray, others light brownish red; primary and secondary coverts in varying stages of emergence with long brownish red down attached to the feathers; primary and secondary feathers dark gray; white down attached to the emerging feathers on the femoral and ventral tracts; pinfeathers emerging on the capital tract.


5 days
one day
11 days
30 days
17 days
24 days

Louisiana Heron
at different days of age



### Unfeathered Parts

Some exposed light pinkish gray skin on lower abdomen. Upper mandible dark gray all over, small area near tip light horn; tip black, inside nostril dark red. Lower mandible dark gray, pinkish along cutting edge, light horn near the dark tip. Iris off-white, pupil black, eye-ring medium gray. Tarsus and toes light gray-green, pale greenish gray under toes; nails medium horn, light-tipped.

### Measurements

Body length 304.8 mm; wing 85.7 mm flattened, 450.9 mm extended; bill 42.9 mm; tarsus 60.3 mm; middle toe 69.8 mm; longest primary pinfeather 38.1 mm; longest secondary pinfeather 38.1 mm; longest rectrix pinfeather 12.7 mm. Length of emergence from sheath of the fifth primary 20.7 mm, fifth secondary 28.6 mm.

### Behavior

Perches above, or sometimes to one side of, the nest and returns only to be fed; responds to human approach by climbing higher in branches. Clings to the perch when handled, requiring the use of some force to pry loose bill and toes. When returned to the nest, climbs into upper branches immediately. No call notes heard. Easily handled.

## *Age Twenty-four Days*

### Plumage

Head covered with long, light tawny down; head, neck, and body completely covered with feathers, most of which retain long reddish down; top of head and neck reddish or brownish red; mantle medium reddish gray, back medium gray; white feather stripe on front of neck well defined; underparts all white; primary and secondary coverts brownish red to dark gray; primaries, secondaries, and rectrices medium gray. Some feathers just emerging on the spinal tract near the tail; other feathers in the same area partially developed.

### Unfeathered Parts

Upper mandible dark gray, black-tipped; inside nostril dark red; lower mandible dark gray, pale horn-tipped. Iris off-white, pupil black, eye-ring medium gray. Tarsus and toes light grayish green with pale brown on front of tarsus and top of toes; pale greenish gray under toes; nails medium horn, light-tipped.

### Measurements

Body length 419.1 mm; wing 174.6 mm flattened, 736.6 mm extended; bill 63.5 mm; tarsus 82.5 mm; middle toe 73.0 mm; fifth primary 73.0 mm, fifth secondary 76.2 mm, middle rectrix 47.6 mm.

### Behavior

Perches away from the nest, usually in bush tops all day; does not return to the nest to be fed; alert to human approach. When released returns immediately to bush tops using bill and feet and balancing with wings; movement is labored. Utters harsh call note at the approach of a parent. Easily handled but very active. Some inter- and intraspecific quarreling, defending perch area by jabbing with bill. Shows tendency to perch with own species in a mixed heron colony.

## *Age Thirty Days*

### Plumage

Some long, light, tawny down on the head; head, neck, and body completely covered with juvenal feathers; head and neck feathers reddish to brownish red; back medium gray; white feather stripe under the neck intermixed with reddish; underparts white; primary and secondary coverts reddish to dark gray; primaries, secondaries, and rectrices medium gray; some pinfeathers on spinal tract.

### Unfeathered Parts

Upper mandible dark gray, black-tipped; lower mandible dark gray, ivory-tipped. Iris off-white, pupil black; eye-ring medium gray. Tarsus and toes light grayish green; front of tarsus and top of toes brownish; pale greenish gray under toes; nails dark horn, light-tipped.

### Measurements

Body length 444.5 mm; wing 184.1 mm flattened, 787.4 mm extended; bill 69.8 mm; tarsus 88.9 mm; middle toe 82.5 mm; fifth primary 82.5 mm; fifth secondary 88.9 mm; middle rectrix 50.8 mm.

### Behavior

Perches in bush tops all day and is fed there; very alert to human approach; returns quickly to bush tops upon being released. No call notes heard during observation periods. Very active when handled. Some inter- and intraspecific quarreling, defending perch area by jabbing with bill and occasionally raising neck feathers in defensive attitude. Shows tendency to perch with own species in a mixed colony.

# BLACK-CROWNED NIGHT HERON

## *Egg Color*

Bent (*op. cit.*) and Reed (*op. cit.*) described the eggs as having a basic greenish hue. Most of the 55 eggs I recorded in 16 nests were pale blue; some were pale greenish blue; and two nests each had four eggs that were pale cypress-green.

## *Age One Day*

### Plumage

Covered mostly with medium brown down, fading to a grayish brown on the lower back; head and neck down longer and darker brown with white down from the base of the bill up and over the crown, the down feathers over the crown white for the outer half of their length; white down on the femoral tract.

### Unfeathered Parts

Head and neck fleshy pink, lighter in the auricular area, medium pink on crown and sides of neck; medium grayish blue around the eye; body skin medium fleshy pink to bluish pink on the back. Upper mandible fleshy gray proximally to pinkish gray distally, dark-tipped; medium gray line on the cutting edge, orange-pink inside the nostril; egg-tooth present. Lower mandible fleshy gray, dark-tipped. Mouth lining pink to deep pink. Eye rather deep set in protruding dark gray eye-ring; iris pale greenish gray, pupil black. Tarsus and toes medium bluish on top of tarsus, lighter on toes, yellowish flesh under the toes; nails pale ivory with distinct pink cast.

### Measurements

Body length 101.6 mm minimum, 107.9 mm maximum; wing 15.9 mm; bill 14.3 mm; tarsus 17.4 mm minimum, 19.0 mm maximum.

### Behavior

Some head and body movement shortly after hatching, the young bird periodically raising head in short labored motions. After the down has dried in two to three hours, young bird lies motionless, eyes closed during most of the hatching day. No reaction to outside stimuli.

## *Age Six Days*

### Plumage

Head, neck, and body sparsely covered with medium grayish brown down, darker on head and neck; white down on forehead and crown, base of feathers dark; pale gray down on femoral tract. No pinfeathers of juvenal plumage visible.

### Unfeathered Parts

Individuals display two different skin colors: (1) Head fleshy pink, paler in auricular area, light gray-blue over eyes; neck medium pink; body skin pale pinkish gray on back, medium pink on humeral area, pale pinkish gray in abdominal region; (2) body skin medium yellow-green, deeper green on some nestlings; pale yellow-green over eyes fading to fleshy on head; pale greenish gray on abdomen. Upper mandible medium purplish gray proximally; culmen, nostril-arch, and sides pale pinkish gray with dark tip; line on cutting edge medium gray; inside nostril dark red; egg-tooth visible. Mouth lining pink to deep pink. Tarsus and toes pale grayish green on top, dark yellow-green on some nestlings; toes yellowish to pinkish flesh below; nails pale ivory with pinkish cast.

### Measurements

Body length 158.7 mm; wing 25.4 mm; bill 22.2 mm; tarsus 30:2 mm.

### Behavior

Capable of movement, but does not leave nest; docile, easily handled, reacts slightly to movements of human hand near nest; calls repeatedly all day with low harsh note; quiet when handled; begins calling shortly after being returned to nest.

## *Age Twelve Days*

### Plumage

Head and neck covered with long down, distal half of crown feathers are grayish white to white, their base dark gray; body sparsely covered with dark gray down; light gray down on femoral tract and abdominal region. Pinfeathers developing on the capital, spinal, humeral, alar, and femoral tracts, mostly tipped with down.

### Unfeathered Parts

Head and body skin grayish pink, neck and abdomen grayish flesh — some nestlings are more greenish gray in these areas. Upper mandible dark gray proximally; culmen, nostril-arch, and sides pale pinkish gray, deeper pink on the culmen; tip dark; line on cutting edge dark gray; egg-tooth still visible. Lower mandible pale pinkish gray with dark tip; line on cutting edge dark gray to black. Mouth lining pink to deep pink, pale blue distally in lower mandible. Iris pale olive-gray, amber in some nestlings, pupil black; eye-ring black. Tarsus and toes pale grayish green on top and sides; grayish yellow on foot-pad and under toes; nails light horn, ivory-tipped.

### Measurements

Body length 215.9 mm; wing 38.1 mm flattened; bill 33.3 mm; tarsus 44.4 mm; middle toe 42.8 mm; length of longest primary pinfeather 9.5 mm; longest secondary pinfeather 15.9 mm; longest scapular pinfeather 15.9 mm.

### Behavior

Capable of climbing from the nest, often perching above or to one side of the nest for short intervals; spends more time in than out of the nest; calls repeatedly with harsh, sometimes buzzing, notes. When returned to the nest, climbs out using bill, wings, and feet. Sometimes aggressive, striking with bill, when handled.

## *Age Eighteen Days*

### Plumage

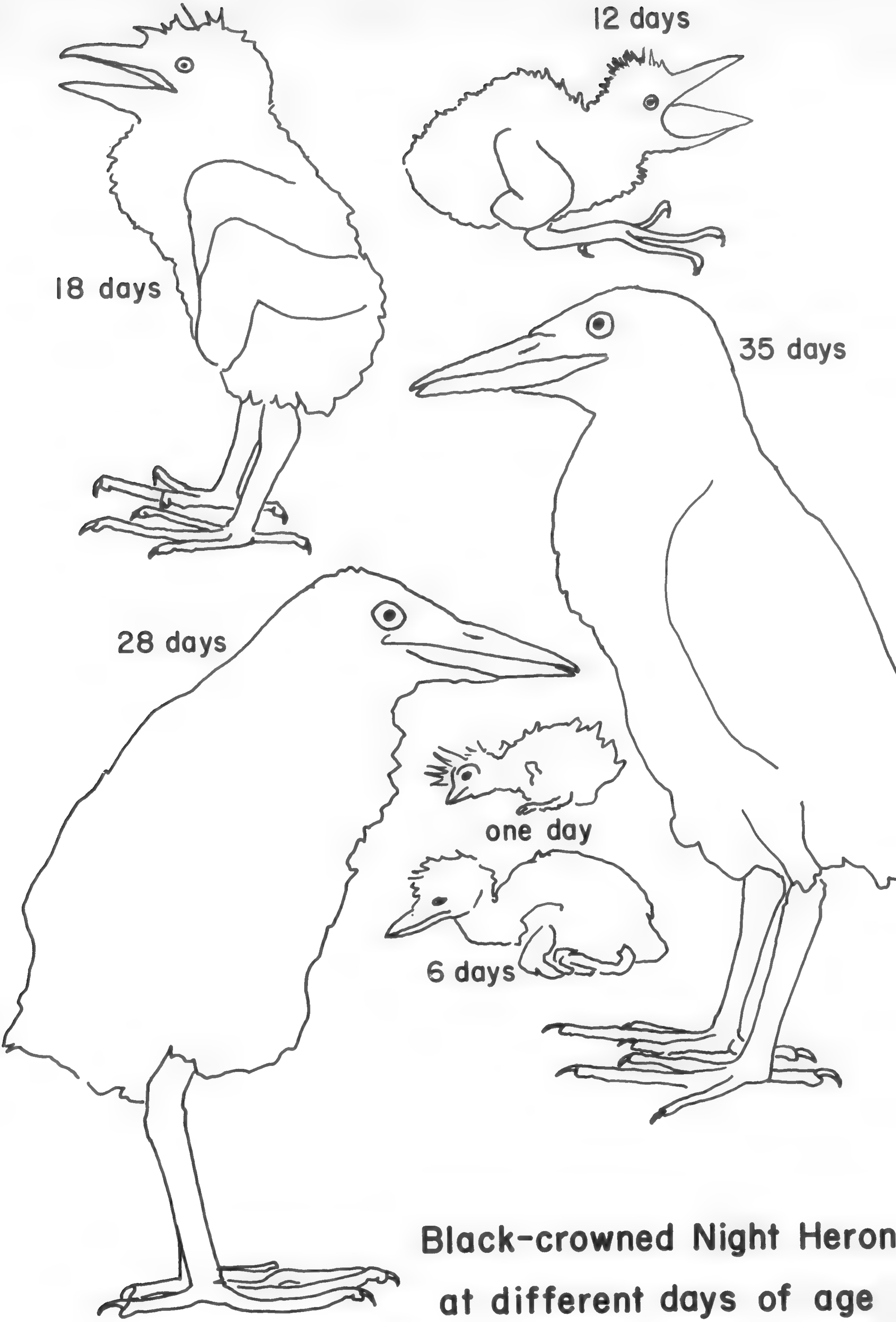
Head, neck, and upper back covered with juvenal feathers, some medium grayish down remaining on these areas; long down on the crown, outer half grayish white to white, base dark gray, interspersed with juvenal feathers. Pale tan and brown feathers just emerging on neck; lower back and abdominal region covered with medium gray down; juvenal feathers emerging through the white to light gray down on the femoral tract; scapulars developing, alternating between dark brown and pale tan; white-tipped primaries and secondaries emerging from sheaths; greater, middle, and lesser coverts also emerging from sheaths, color varying from white to medium and light tan; marginal coverts just emerging from sheaths.

### Unfeathered Parts

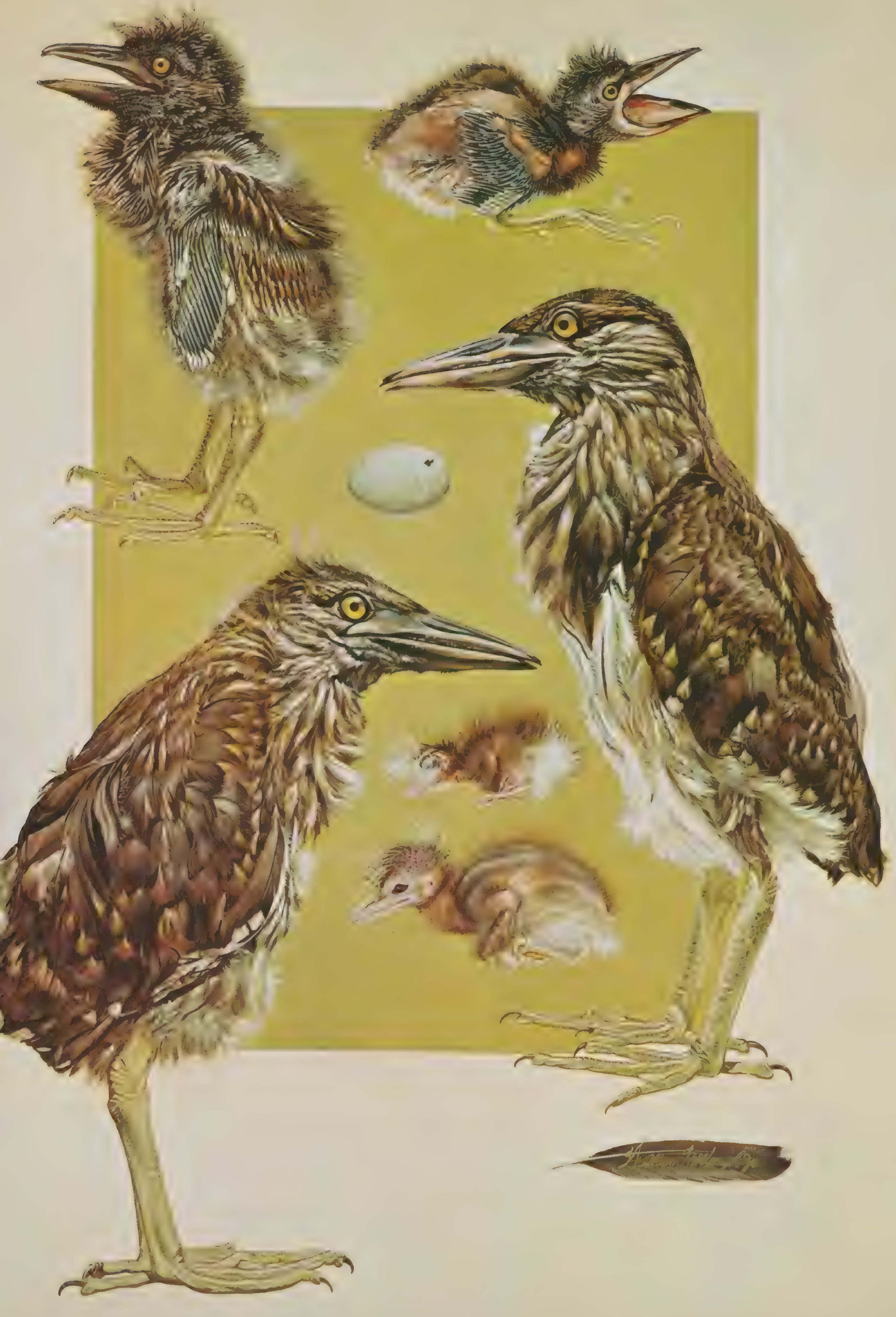
No skin showing, body covered with feathers and down. Upper mandible medium dark gray, darker proximally; culmen dark gray; nostril-arch and sides pinkish gray; dark tip; cutting edge dark gray; egg-tooth visible. Lower mandible pale pinkish gray with rounded sides dark gray proximally, darker distally; ivory tip; cutting edge dark. Iris medium amber, pupil black; eye-ring dark gray. Tarsus and toes medium greenish brown on top and outside, paler on some nestlings; inside of tarsus pale grayish green, grayish yellow under toes; nails medium horn, ivory-tipped.

### Measurements

Body length 304.8 mm; wing 107.9 mm flattened; bill 38.1 mm; tarsus 63.5 mm; middle toe 63.5 mm; longest primary pinfeather 28.6 mm; longest secondary pinfeather 28.6 mm; length of emergence of vanes from sheath of fifth primary 6.3 mm, from sheath of fifth secondary 15.9 mm; longest scapular 23.8 mm.


12 days
18 days
35 days
28 days
one day
6 days

Black-crowned Night Heron
at different days of age



### Behavior

Perches near nest, returning to be fed; alert to human approach, often climbing into higher branches; somewhat aggressive when handled; climbs into higher branches when returned to nest; infrequent low harsh call notes heard during the day.

## *Age Twenty-eight Days*

### Plumage

Crown covered with long down, outer half white, base dark brown; upper neck covered with short, medium brown down; head, neck, and body completely covered with feathers, most of which retain light to medium tan or dark brown down; all contour feathers streaked with V-shaped color patches, some more elongated or wedge-shaped, varying from off-white to buffy to medium tan; scapular feather-streaking wedge-shaped, off-white to buffy to medium tan, with the more dorsal feathers marked with the deeper color; streaking of primary and secondary coverts V-shaped, off-white to buffy; developing primaries tipped in white, most of white on outer vane, the tipping receding in prominence from tenth to first primary; secondary feather-tipping obscure, white diminishing to no white on Secondary 5; however, amount and intensity of white tipping on both primaries and secondaries varies in young birds; rectrices medium gray color, with off-white edging and tipping; down-like covering of throat is an intermixture of dark brown feathers streaked with off-white and off-white feathers streaked with dark brown; white breast feathers with well-defined dark gray wedge-shaped streaks, less boldly streaked on abdominal area; femoral tract feathers grayish brown, some streaking present.

### Unfeathered Parts

Upper mandible dark gray proximally; culmen dark gray; nostril-arch pinkish gray, rounded sides ivory; tip black; cutting edge black; egg-tooth still visible. Lower mandible warm ivory with rounded side dark gray proximally; irregular dark spot distally; light ivory tip. Iris medium amber, pupil black; eye-ring dark gray. Tarsus and toes pale grayish green; scales outlined with light brown, deeper greenish brown on outside of tarsus, lighter on inside; toes similar to the major investment scales; grayish yellow under toes; nails medium horn, ivory-tipped.

### Measurements

Body length 431.8 mm; wing 177.8 mm flattened, 787.4 mm extended; bill 57.1 mm; tarsus 88.9 mm; middle toe 88.9 mm; length of emergence from sheath of fifth primary 38.1 mm; emergence of fifth secondary 44.4 mm, of longest rectrix 38.1 mm.

### Behavior

Perches above the nest and is fed there; alert to human approach, climbs into higher branches; displays some aggression when handled, opening bill and raising crown and neck feathers; immediately climbs to upper branches when released; no call notes heard during the day.

## *Age Thirty-five Days*

### Plumage

Some down on crown and nape, outer half white, base dark brown; head, neck, and body completely covered with feathers, short down remaining on the mantle and wing coverts. Some pinfeathers just emerging from sheaths.

### Unfeathered Parts

Upper mandible dark gray proximally; culmen dark gray; nostril-arch dull gray, rounded sides ivory; tip black; cutting edge black; egg-tooth still visible. Lower mandible ivory with rounded sides darker, fading to dull medium gray proximally; irregular dark spot distally; light ivory tip. Iris medium amber, pupil black; eye-ring light gray. Tarsus and toes pale greenish gray; scales outlined with light brown, deeper grayish green scales on outside of tarsus (some young birds have more brownish scales on top and outside of tarsus), lighter on the inside; toes similar to the major investment scales, grayish yellow under toes; nails medium horn with darker tipping.

### Measurements

Body length 469.4 mm; wing 228.6 mm flattened, 939.8 mm extended; bill 61.9 mm; tarsus 92.0 mm; middle toe 88.9 mm; length of emergence from sheath of fifth primary 95.2 mm; emergence of fifth secondary 76.2 mm; of longest rectrix 76.2 mm.

### Behavior

Perches on bush tops all day and is fed there; alert to human approach and avoids capture. Sometimes aggressive when handled, but also receptive to gentle handling; immediately climbs to upper branches when released; no call notes heard during the day.

# COMMON EGRET

## *Egg Color*

The 21 eggs from eight nests were all pale blue to pale greenish blue, unlike the descriptions by Bent (*op. cit.*) and Reed (*op. cit.*) who give the egg color as basically green.

## *Age One Day*

### Plumage

Covered dorsally with long white down, longer on the forehead and crown; down very sparse ventrally.

### Unfeathered Parts

Orbital region pale gray-blue; eye-ring gray, eyelid warm gray to pale gray-blue; forehead and crown dark blue-gray; throat pinkish, under neck bluish pink fading to bluish gray on top of neck; body dark blue-gray dorsally, lighter ventrally; humeral region pinkish flesh varying with individuals from grayish flesh to pinkish flesh with a decidedly blue cast. Upper mandible pale warm gray proximally; culmen dark gray to black; nostril-arch warm gray; rounded sides dark gray proximally, black distally; cutting edge gray; inside nostril pink to yellow-pink; tip black; egg-tooth visible. Lower mandible pinkish yellow to grayish yellow; dark spot on rounded sides distally; cutting edge dark. Mouth lining pink to deep pink; tongue pink with dark gray tip. Eye rather deep set in protruding eye-ring; iris off-white, pupil black. Tarsus and toes pale pinkish flesh with bluish cast, lighter underneath; foot pad pinkish gray; nails pale ivory, hallux darker.

The Handbook of North American Birds (*q. v. supra*) describes the "apteria, mandibles, legs, and feet yellowish green" in the newly hatched Common Egret. None of the 21 hatchlings fitted this description; they showed no change in skin color until three days old, at which time I recorded the following colors: orbital area gray-blue; crown gray; nape yellow to pinkish yellow; body pale gray-green; bill fleshy pink; tarsus grayish green; toes fleshy pink.

### Measurements

Body length 114.3 mm minimum, 127.0 mm maximum; bill 12.7 mm minimum, 14.3 mm maximum; tarsus 19.0 mm minimum, 20.6 mm maximum.

### Behavior

Just after hatching and while the down is still moist, the nestling can hold its head up and move its body in abrupt motions. Down dries in two to three hours; little or no reaction to human stimuli; very docile; no call notes heard during the first day; very weak peeping notes heard during the second and third days.

## *Age Seven Days*

### Plumage

Head, neck, and body covered with white down, longer on forehead and crown; pinfeathers on most feather tracts, those on crown and neck emerging, some down-tipped; humeral tract feathers well formed, down-tipped; on alar tract covert feathers emerging, primary and secondary feathers just emerging; femoral tract feathers emerging, down-tipped.

### Unfeathered Parts

Orbital region yellow, fading to greenish gray on the crown; eye-ring grayish yellow; neck medium gray; body yellowish green dorsally with some individuals more greenish, grayish green ventrally; wing gray to gray-green. Upper mandible yellow including the nostril-arch; rounded sides deeper yellow; dark gray streak extending from under the eye to one-half length of the bill; cutting edge dark; black tip; egg-tooth visible; lower mandible yellow, deeper yellow along the cutting edge and at the tip. Mouth lining pink to deep pink; iris off-white, pupil black. Tarsus and toes medium gray to greenish gray, toes lighter; yellowish gray under toes; scales forming on tarsi and toes.

### Measurements

Body length 171.4 mm; wing 31.7 mm flattened; bill 19.0 mm; tarsus 30.2 mm; middle toe 22.2 mm.

### Behavior

Quiet most of the day; some movement in the nest; docile when handled. Weak calls during the day are repeated in series, followed by quiet periods; silent for about one hour after being returned to the nest. Fed in the nest.

## *Age Fourteen Days*

### Plumage

Head, neck, and body covered with white down, longer on forehead and crown; pinfeathers on all tracts, all down-tipped except greater wing coverts.

### Unfeathered Parts

Orbital region yellow, fading to greenish on the crown; eye-ring grayish yellow; neck and body green dorsally (some individuals bluish green to grayish green), grayish green ventrally; wing gray to grayish green. Upper mandible yellow, rounded sides deeper yellow; black streak extending anteriorly from under the eye to three-fourths the length of the bill; cutting edge dark; tip black; egg-tooth visible. Lower mandible yellow, rounded sides lighter yellow proximally. Iris off-white, pupil black. Tarsus and toes pale gray, light gray under toes; nails medium horn, tipped light gray. Scales well formed on tarsi and toes.

### Measurements

Body length 254.0 mm; wing 34.9 mm flattened; bill 31.7 mm; tarsus 39.7 mm; middle toe 69.8 mm; length of longest primary pinfeather 9.5 mm; longest secondary pinfeather 9.5 mm; length of emergence from sheath of longest scapular 12.7 mm.

### Behavior

Quiet most of the day; alert to human approach, remains in the nest; docile when handled and crouches when returned to the nest. Intermittent call notes heard during the day, repeating the calls much faster as the parent approaches with food.

## *Age Twenty-one Days*

### Plumage

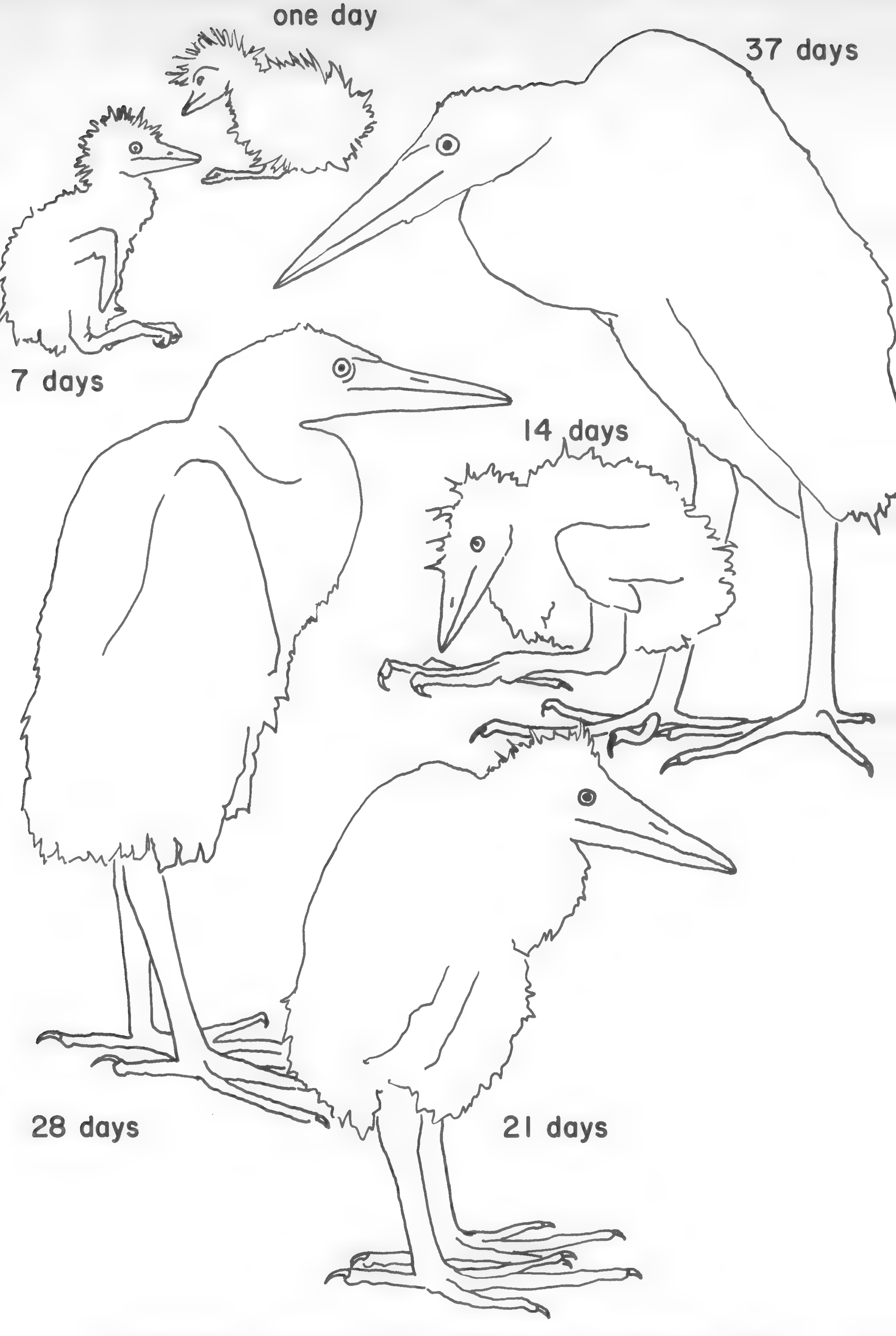
Head, neck, and body, except crural region, covered with soft, down-like, white feathers. White down present on head, neck, and back, longest on the forehead; pinfeathers of crural region emerging from sheaths.

### Unfeathered Parts

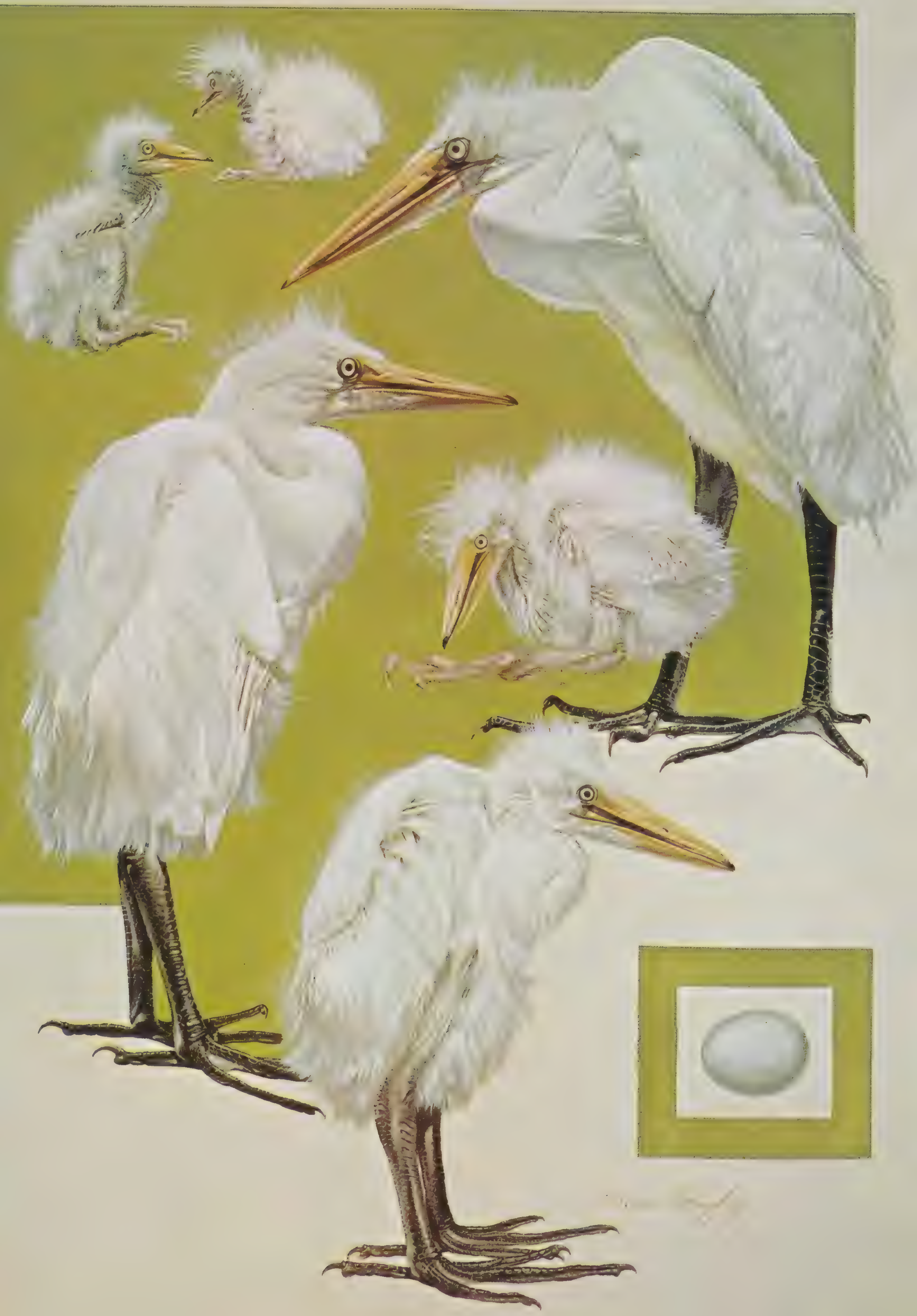
Eye-ring yellow; upper mandible yellow, rounded sides deeper yellow; black streak extending anteriorly from under the eye to three-fourths the length of the bill; cutting edge dark; tip black; egg-tooth still visible. Lower mandible yellow, rounded side lighter yellow proximally. Iris off-white, pupil black. Tarsus and toes dark gray, light gray under toes; nails medium horn, tipped light gray.

### Measurements

Body length 377.1 mm; wing 120.6 mm flattened, 469.9 mm extended; bill 63.5 mm; tarsus 82.5 mm; middle toe 85.7 mm; length of emergence from sheath of fifth primary 19.0 mm; emergence of fifth secondary 15.9 mm.


one day
37 days
7 days
14 days
28 days
21 days

Common Egret at different days of age



### Behavior

Alert to human approach; remains in or near the nest all day; returns to the nest to be fed; docile when handled; makes little or no attempt to leave nest when returned. No call notes heard during the day.

## *Age Twenty-eight Days*

### Plumage

Head, neck, and body covered with white juvenal feathers. White down on head, neck and back, longest on the forehead.

### Unfeathered Parts

Eye-ring grayish yellow; soft parts of bill yellow. Upper mandible yellow, rounded sides deeper yellow; black streak extending anteriorly from under the eye to two-thirds the length of the bill; cutting edge dark; tip black. Lower mandible yellow; tip black. Iris off-white, pupil black. Tarsus and toes deep gray, almost black; gray under toes; nails medium dark horn, tipped light gray.

### Measurements

Body length 508.0 mm; wing 177.8 mm flattened, 762.0 mm extended; bill 66.7 mm; tarsus 95.2 mm; middle toe 92.0 mm; length of emergence from sheath of fifth primary 38.1 mm; emergence of fifth secondary 41.3 mm; emergence of longest scapular 38.1 mm.

### Behavior

Alert to human approach; remains near the nest all day, usually in branches above; does not return to the nest to be fed; docile when handled, climbing to upper branches when released. No call notes heard during the day.

## *Age Thirty-seven Days*

### Plumage

Head, neck, and body completely covered with white juvenal feathers. White down on head and neck, longest on the forehead; some down still remaining on the back.

### Unfeathered Parts

Eye-ring grayish yellow. Upper mandible yellow, rounded sides deeper yellow; black streak extending anteriorly from under the eye to one-half the length of the bill; cutting edge dark; black tip. Lower mandible yellow, rounded sides yellow; small black tip. Iris off-white, pupil black. Tarsus and toes black; gray under toes; nails medium dark horn, tipped gray.

### Measurements

Body length 596.9 mm; wing 228.6 mm flattened, 1,054.1 mm extended; bill 74.6 mm; tarsus 114.3 mm; middle toe 95.2 mm; fifth primary 101.6 mm; fifth secondary 76.2 mm; middle rectrix 63.5 mm.

### Behavior

Alert to human approach, will fly 10—15 feet over bush tops; remains in bush tops all day; docile when handled; climbs to branch tops immediately when released. No call notes heard during the day.

# LITTLE BLUE HERON

## *Egg Color*

The color agrees with Bent (*op. cit.*) as being "pale bluish green, varying from 'light Niagara green' to 'lichen green'."

## *Age One Day*

### Plumage

Covered dorsally with very pale gray down, longer tawny tipped filaments on the forehead and crown; down sparse ventrally.

### Unfeathered Parts

Skin of orbital region medium gray-blue; forehead dark blue-gray; crown pink; throat pinkish flesh; neck medium to dark pinkish gray; body dark gray dorsally, lighter ventrally. In some nestlings, the skin is a light flesh-gray dorsally, specifically on the neck and in the femoral region; these lighter nestlings also have a lighter colored bill at hatching; body skin and bill begin to darken at age four to six days, assuming a more "normal" coloration. Culmen and rounded sides of upper mandible pinkish gray proximally and extending distally to a dark pinkish blue tip; nostril-arch lighter; cutting edge very light gray distally; inside nostril pink; egg-tooth present. Lower mandible pink proximally; bluish pink distally, with light ivory tip. Bills of day-old nestlings vary, some slightly darker than others; an occasional nestling is found with a pale flesh-gray bill and no dark tip. Mouth lining pink. Eye rather deep set in a protruding gray eye-ring; iris light gray to pale tan, pupil black. Tarsus and toes medium gray; toes lighter, some tarsi flesh-gray or pinkish gray; pale pink or pale gray yellow under toes; nails pale ivory with blue cast.

### Measurements

Body length 76.2 mm minimum, 88.9 mm maximum; bill 11.1 mm minimum, 12.7 mm maximum; tarsus 19.0 mm.

### Behavior

Soon after hatching the nestling raises its head, moves the body in short, abrupt motions; down dries in two to three hours. During the first day little or no reaction to my presence at the nest.

## *Age Seven Days*

### Plumage

Head and body covered with white down, longer on the forehead and crown; all feather tracts with emerging juvenal feathers, more pronounced for scapulars and wings; feathers down-tipped; juvenal feathers just emerging on crown.

### Unfeathered Parts

Exposed skin on throat and under neck pinkish flesh — top of neck yellow-green on some young; orbital region gray-blue; crown pink; humeral region dark pinkish gray, lighter on abdominal area — some nestlings' body skin may be blue-gray, green-gray, yellowish green-gray. On upper mandible, culmen and rounded sides pale pinkish gray proximally, pale bluish pink fading to blue-black tip distally; nostril-arch pale pinkish gray; cutting edge bluish pink; inside nostril pink to deep pink; egg-tooth present. Lower mandible pale pinkish gray proximally fading to pale blue terminated by a small dark spot distally; tip ivory. Individuals have slightly deeper colored bills: more gray, pale blue-gray, pale yellow-gray, or pale green-gray. Mouth lining pink to deep pink. Iris pale gray to off-white, pupil black; eye-ring gray. Tarsus and toes medium gray-blue with pink cast; foot-pad and under side of tarsus pale gray; toes pale pinkish gray to pale yellow-gray below; nails pale horn, ivory-tipped; scales just forming on tarsi and toes. Some young have paler tarsi and toes pale gray-green.

### Measurements

Body length 165.1 mm; wing 34.9 mm flattened; bill 25.4 mm; tarsus 34.9 mm; middle toe 28.6 mm; length of longest primary pinfeather 6.3 mm; longest secondary pinfeather 6.3 mm; longest scapular pinfeather 6.3 mm.

### Behavior

Capable of movement in the nest, changing positions but remaining still most of the time during the observation period; easily handled, docile, some slight reaction to hand movement; remains quiet for ten to fifteen minutes after being returned to the nest. Young calls repeatedly with a weak peeping note at intervals during the day.

## *Age Twelve Days*

### Plumage

Head, neck, and body completely covered with juvenal feathers; white down interspersed among the head and body feathers, longer on the forehead and crown; considerable down on the back and femoral area; some down remaining in the abdominal region; capital tract juvenal feathers emerging, down-tipped. Juvenal feathers on the neck ventral tract emerged, longest feathers posteriorly, some down-tipped; scapulars, primaries, secondaries, coverts, and ventral body feathers well formed, all down-tipped.

### Unfeathered Parts

Exposed body skin medium gray — some nestlings green-gray or yellowish green-gray — dorsally, lighter gray ventrally. Upper mandible pale pinkish gray proximally; culmen, rounded sides, and nostril-arch pale gray with pinkish cast fading to light pinkish blue distally; darker tip; egg-tooth visible. Lower mandible pale pinkish gray proximally fading to a pale bluish gray distally. Some individuals have pale yellow-gray replacing the pinkish gray on both mandibles; some bill tips are darker — upper tip black. Mouth lining pink with black line along cutting edges. Iris pale gray to off-white, pupil black; eye-ring gray. Tarsus and toes pale greenish gray — some nestlings bluish gray; pale gray or yellowish gray below; foot-pad yellow-gray; nails pale to medium horn, ivory-tipped; scales forming on tarsi and toes.

### Measurements

Body length 228.6 mm; wing 63.5 mm flattened; bill 31.7 mm; tarsus 47.6 mm; middle toe 53.9 mm; length of longest primary pinfeather 15.9 mm; longest secondary pinfeather 15.9 mm; longest scapular pinfeather 12.7 mm.

### Behavior

Capable of climbing from the nest; perches on the side of, or near, the nest most of the day; returns to the nest to be fed; when returned to the nest, climbs out into upper branches immediately; shows some fear when handled. Calls intermittently during the day.

## *Age Seventeen Days*

### Plumage

Head and neck covered with long white down; capital tract feathers down-tipped; orbital and auricular area feathers showing down tips; heavy, white, down-like juvenal feathers emerging on lower neck; back, wings, and abdominal region covered with down-like white feathers; crural tract feathers partly developed, down-tipped; the shank is the only area — excluding around the eye, ear, and upper neck — not full covered with feathers.

### Unfeathered Parts

Dark gray or dark green-gray skin shows through the developing feathers. Culmen, nostril-arch, and proximal area of upper mandible yellow or yellow-gray, extending to a black tip distally; rounded sides dark gray, cutting edge lighter; inside nostril deep pink. Lower mandible yellow to yellow-gray proximally fading through deep yellow-gray on the rounded sides to a black tip terminated by pale to deep ivory outline. Some individuals have a definite gray or pinkish gray bill with a medium dark tip. Iris very pale gray to off-white, pupil black; eye-ring pale gray often with bluish cast. Tarsus and toes light gray-green, deeper on the toes, pale yellow-gray below; foot-pad yellow, back of tarsus pale yellow; nails medium horn, ivory-tipped; scales well formed on tarsi and toes.

### Measurements

Body length 254.0 mm; wing 82.5 mm flattened, 419.1 mm extended; bill 47.5 mm; tarsus 53.97 mm; middle toe 63.5 mm; length of emergence from sheath of fifth primary 22.2 mm; emergence of fifth secondary 25.4 mm; emergence of longest scapular 25.4 mm; emergence of longest rectrix 12.7 mm.

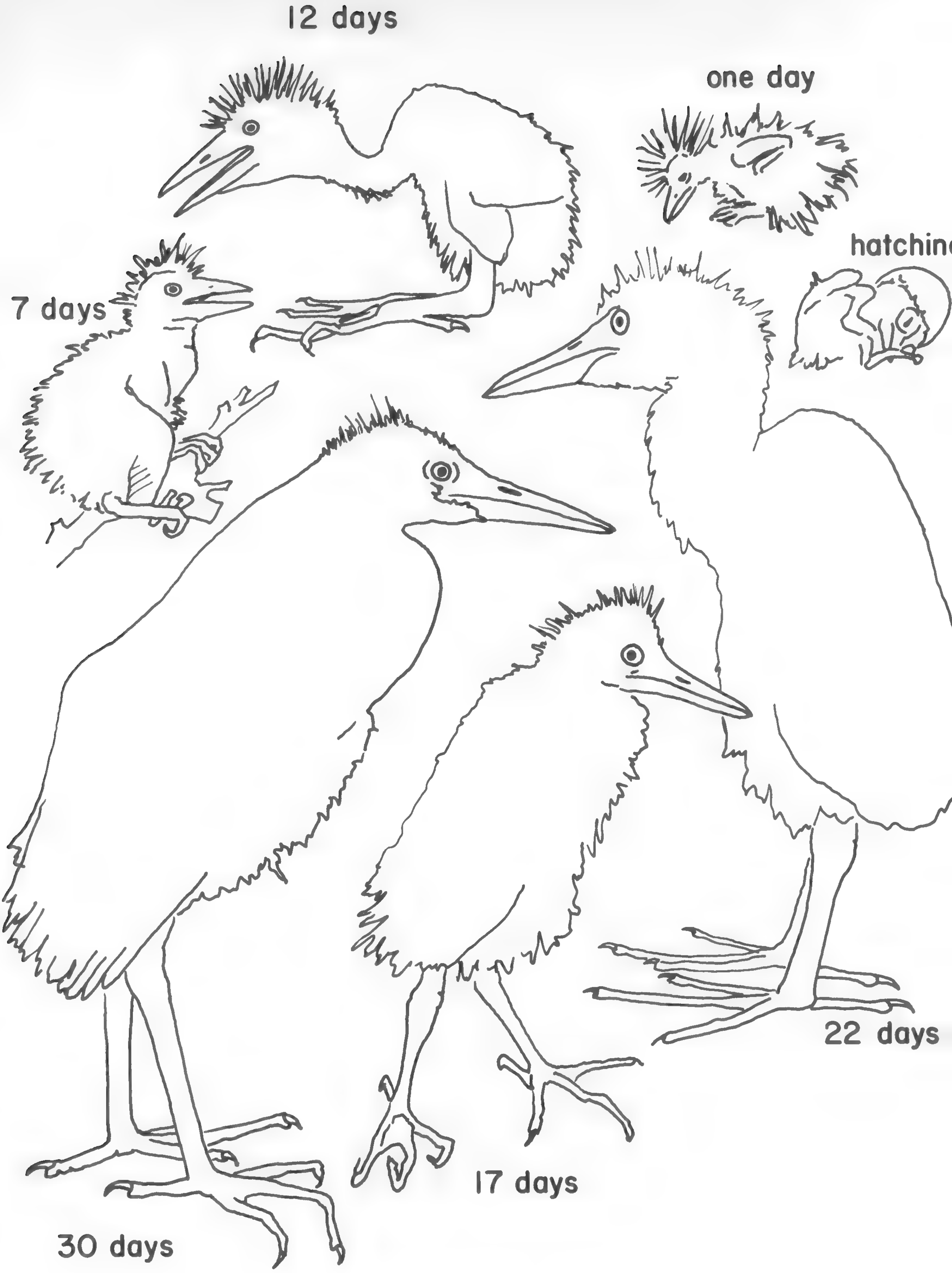
### Behavior

Perches away from the nest, sometimes returning to be fed, or moves to parent bird for feeding; alert to human approach and climbs to higher branches; clings to branches with bill and toes when caught; easily handled; upon release climbs with some labored movement to upper branches using bill, wings, and feet.

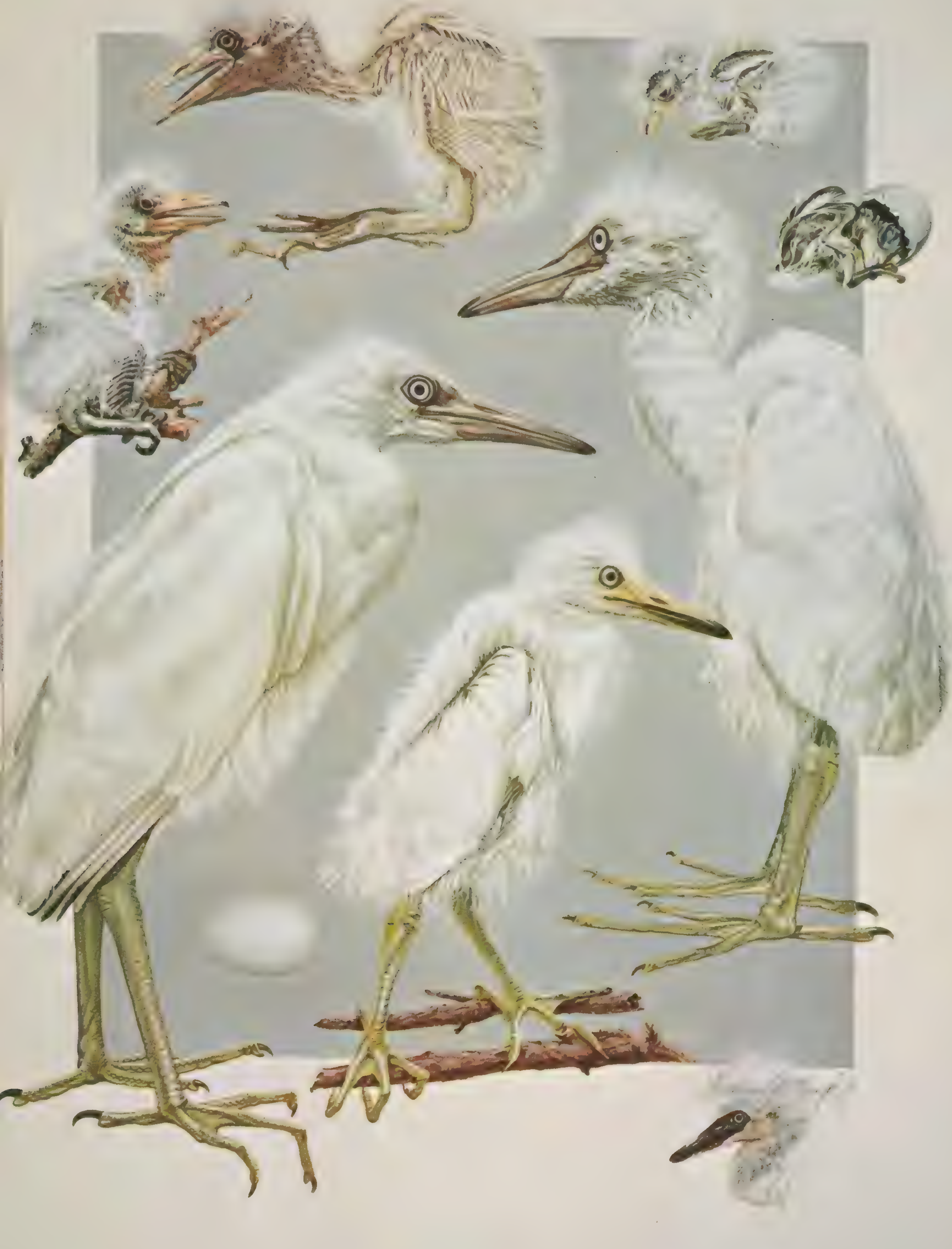
## *Age Twenty-two Days*

### Plumage

Forehead and crown covered with long white down and well-developed juvenal feathers, down-tipped, cover head and upper neck; lower part of neck and body completely covered with


12 days
one day
hatchin
7 days
22 days
17 days
30 days

Little Blue Heron
at different days of age



white juvenal feathers; Primaries 4–8 showing dark tips, medium gray (inner vane), dark gray (outer vane).

### Unfeathered Parts

On upper mandible culmen pinkish gray fading to a deeper gray distally; nostril-arch and rounded sides bluish gray; cutting edge dark; dark gray tip. Lower mandible pinkish gray proximally; rounded sides pinkish gray fading to a bluish gray distally; dark gray tip terminated with warm ivory outline; some individuals have a yellow or pale gray-yellow bill, showing evidence of changing to "immature gray." Iris very pale gray to off-white, pupil black; eye-ring pale warm gray, pale blue behind eye. Tarsus and toes light gray-green, toes sometimes darker; foot-pad yellow, back of tarsus pale yellow to light gray posteriorly; toes pale yellow-gray to gray below; nails medium horn, ivory-tipped; scales completely formed on tarsi and toes.

### Measurements

Body length 361.9 mm; wing 177.8 mm flattened, 749.3 mm extended; bill 53.9 mm; tarsus 76.2 mm; middle toe 73.0 mm; length of emergence from sheath of fifth primary 66.7 mm; emergence of fifth secondary 69.8 mm; emergence of longest rectrix 34.9 mm.

### Behavior

Perches in bush tops all day and is fed there; alert to human approach, easily handled, and, when released, climbs to bush tops immediately using wings, bill, and feet. Calls with harsh note. Some intraspecific quarreling. Raises crown feathers and defends perch with jabbing bill. Usually perches with own species in a mixed colony.

## *Age Thirty Days*

### Plumage

Some long white down remaining on forehead and crown; head, neck, and body completely covered with white juvenal feathers; Primaries 2–8 showing dark tips; inner and outer primary vanes dark gray except Primary 2 which has no color on inner vane.

### Unfeathered Parts

On upper mandible, culmen pinkish gray fading to a deeper gray distally; nostril-arch and rounded sides bluish gray; cutting edge black; tip dark gray to black. Lower mandible pinkish gray to gray proximally; rounded sides pinkish gray to bluish gray distally; dark gray tip terminated with ivory outline. Iris very pale gray to off-white, pupil black; eye-ring pale warm gray, pale blue behind eye. Tarsus and toes pale to light gray-green, tarsus showing deeper greenish gray above; tarsus color varies in some individuals to a deeper gray-green; foot-pad pale yellow; back of tarsus pale yellow to pale yellow-gray; toes pale yellow-gray to pale gray below; nails medium horn, ivory-tipped.

### Measurements

Body length 444.5 mm; wing 215.9 mm flattened, 838.2 mm extended; bill 57.1 mm; tarsus 88.9 mm; middle toe 76.2 mm; length of emergence from sheath of fifth primary 127.0 mm; emergence of fifth secondary 133.3 mm; emergence of longest rectrix 44.4 mm.

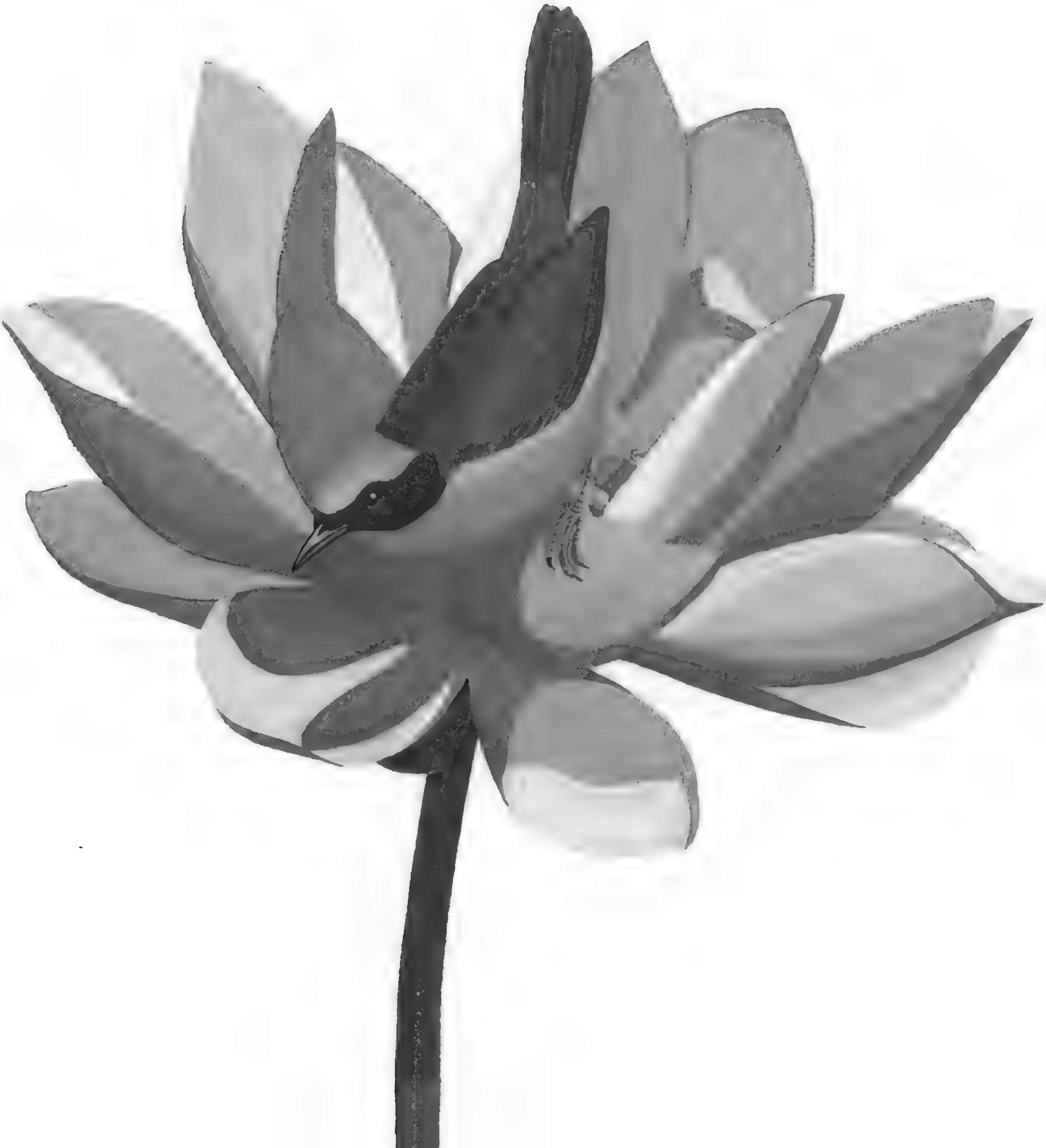
### Behavior

Perches in bush tops all day and is fed there; very alert to human approach; easily handled and quickly climbs back to bush tops when released. No call notes heard during observation periods. Some inter- and intraspecific quarreling, defending perch with bill-jabbing, raising crown and neck feathers in defensive attitude. Usually perches with own species in mixed colony.

*Acknowledgments*

For making this study possible, I am grateful to the managers of Pea Island National Wildlife Refuge in North Carolina, William Good and Jerry Holloman, and to the Regional Office of the U. S. Fish and Wildlife Service in Atlanta, Georgia.

c/o MRS. DONALD KRUSE, 331 WEST PONTIAC, FORT WAYNE, INDIANA 46807



Masked Yellowthroat, *Geothlypis aequinoctialis*. Painting by Godfrey R. Bourne.

# THE BLUE DUCK OF NEW ZEALAND

### Janet Kear

One can find no better introduction to the Blue Duck (*Hymenolaimus malacorhynchos*) than the quotation from Buddle (1951): "To those who know it . . . , the memory of that long-drawn-out whistle, *'whio,'* the call of the blue duck will bring a nostalgia, a longing to be back once more in the heart of the bush, high up in the beech forest, with the bare mountain tops glimpsed through a gap in the canopy; a rushing torrent cascading over huge boulders and broken rock, with here and there a still pool; the only sound that of the water, . . . such is the home of the blue duck."

The Blue Duck (Figures 1 and 2), one of the least known of the waterfowl, inhabits one of the world's loneliest and loveliest regions, the high country of New Zealand. Taxonomically something of a puzzle, the Blue Duck behaves little like the other dabbling ducks, with which it is usually placed, and appears to share its food niche with fresh-water fish (Kear and Burton, 1971). The drake, although highly territorial and aggressive, apparently mates for life and shares in the care of the ducklings.

The Blue Duck is astonishingly tame and confiding, often allowing a person to approach closely before taking off in flight. Yet despite its tameness, few people have studied it. According to Blackburn (1967), the vast majority of New Zealanders have never seen this unique bird, and many are unaware of its existence.

The following account deals with my brief study of the Blue Duck in the field between October 1968 and January 1969, brings together all the records of its breeding biology, and considers its taxonomic position in the light of our present knowledge.

## *Description*

The Blue Duck is, as its name implies, basically blue in color — a dark slate blue, not unlike that of the water and the wet rocks against which it most often appears. Its crown is tinged with green. The feathers of its breast and upper abdomen are richly spotted with chestnut, and so beautiful that Maori women formerly wore them as ornaments around the neck. The wing is the same lead blue with the tips of the six outer secondaries narrowly bordered with white, the only remnants of the speculum which, in most dabbling ducks, extends over nine or 10 secondaries. Four or five of the innermost secondaries,

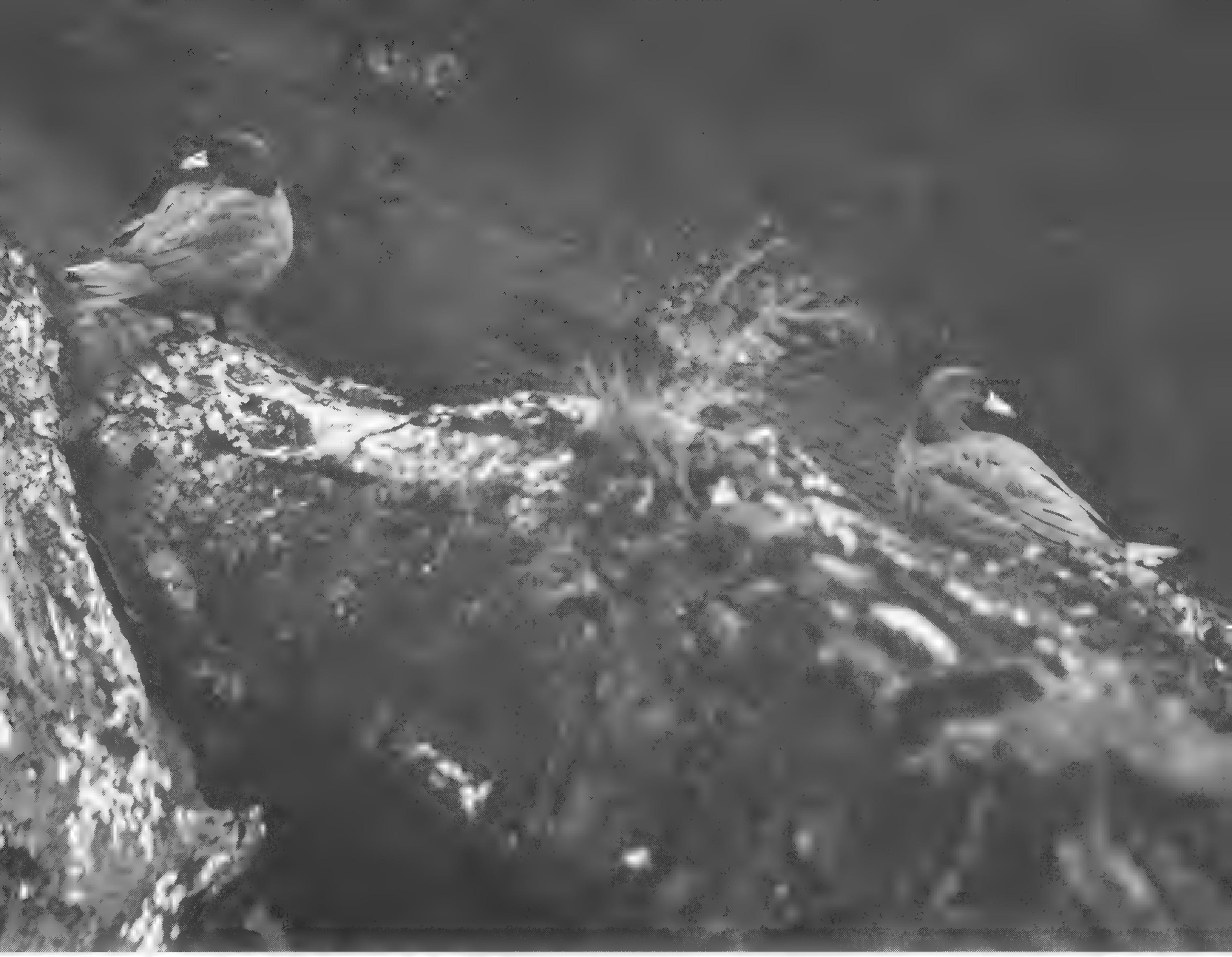


Figure 1. A pair of Blue Ducks standing above the waters of a mountain stream. A large and tame duck, it lives only in New Zealand. Courtesy of National Publicity Studios, Wellington.

sometimes called "tertials," have a longitudinal black line on the outer margin. When the wing is folded, hiding the speculum, these slightly iridescent, velvety markings are still visible. The legs and feet are dark brown, and the eyes a bright golden yellow.

The Blue Duck has one of the most peculiar bills of all the Anatidae. Mainly white, it is edged in black, and from the forward, or anterior, edges of the upper mandible rise a pair of soft black flaps (Figure 3), which overhang the lower jaw to a considerable extent and probably cushion the edges of the bill when the bird feeds (Kear and Burton, 1971).

Except in voice and size, the male and female are not readily distinguishable. The drake gives a long, drawn-out whistle, from which the species derives the Maori name of Whio; the female utters only a low rasping quack. On the average, the male is somewhat heavier than the female (Table 1).

## *Habitat*

The Blue Duck, now mainly confined to the mountain regions of New Zealand, is even more strictly associated with water than most other ducks (Figure 4). In the bush, from sea level to tree line, it inhabits the swift, clear streams: " . . . where the foaming torrent, walled in on both sides, rushes impetuously over its shingle-bed, surging around the huge water-worn boulders that obstruct its course, and forming alternately shallow rapids and pools of deep water" (Buller, 1888). The clean, well-oxygenated water in the turbulent streams that Buller described supports an abundance of invertebrate life that, in turn, supports the Blue Duck. The food supply seems to be one factor restricting the duck to a certain stream; the width of the stream another. Blue Ducks probably live permanently only on streams over 10 feet wide in places, although they certainly use smaller streams for feeding.

While difficult to find, the Blue Duck, with its patchy but wide distribution, is fortunately in no immediate danger of extinction. In the North Island, it inhabits mainly the mountain regions around Urewera and Tongariro National Parks. I spent most of my time in Urewera. On the South Island, the Blue Duck occurs throughout the western uplands, principally in Otago and Southland. Figure 5 shows the Blue Duck's recent distribution and all the sites where sub-fossil bones have been found (R. J. Scarlett, pers. commun.). Three sites were middens of moa-hunting Polynesians, probably indicating that the early inhabitants of New Zealand ate these ducks but never commonly. Only one of the remaining sites, all in caves and potholes, lies within the bird's present range. Mr. Scarlett (pers. commun.), although he knows of no true fossil remains of the Blue Duck, believes that the genus has been confined to New Zealand for many thousands of years.

We cannot assess the total number of Blue Ducks at the present time. The almost complete dependence of the species upon the streams and rivers of forested areas at any altitude and the bird's high degree of territoriality automatically restrict and localize the populations. Probably no more than one breeding pair occurs within each half mile of unmodified bush stream of suitable width. However, this vague estimate requires additional study and checking by banding groups of birds. New Zealand has thousands of acres of bush and many miles of seemingly suitable streams.

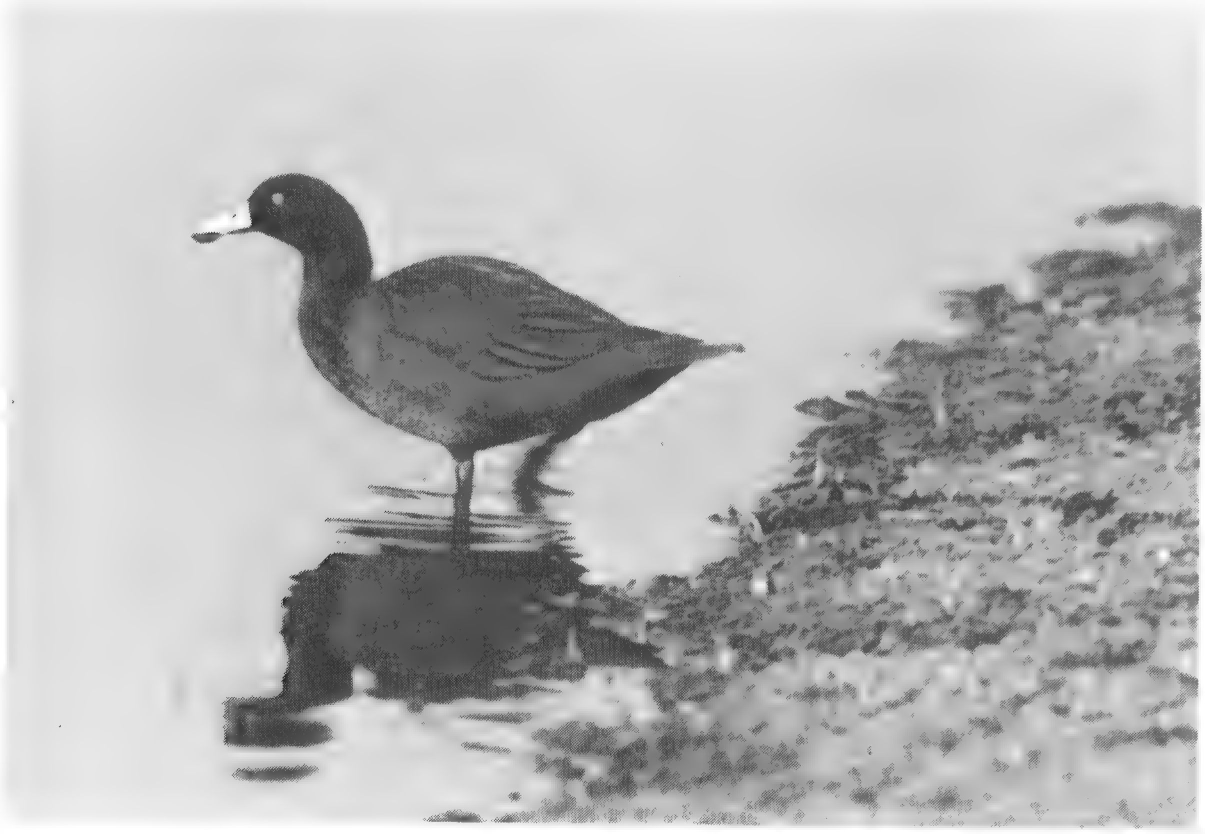


Figure 2. The Blue Duck has a strong bluish sheen to its dark gray body. The breast is heavily spotted with reddish brown. And the distinctive bill is pinkish white with a black tip. Photograph by E. E. Jackson.

During the last century, the Blue Duck not only has disappeared from parts of its former range, but also is less common within its present range. Buller (1888) wrote that soldiers, engaged in the war of 1869–1871 against the Maori Te Kooti, sometimes took 30 or 40 Blue Ducks in a day in Urewera country. I could not even see that number when I searched there in 1968. Phillips (1926) noted that the bird still lived on streams within 30 miles of Wellington; alas, this is no longer true.

Although easy to capture and, therefore, at times slaughtered quite ruthlessly, the Blue Duck's decline has undoubtedly been due more to the destruction of its habitat than to killing. The clearing of land for agriculture definitely expelled the birds from those areas (Guthrie-Smith, 1927). The cutting of the bush and letting in the sun altered the stream environment by warming it and by increasing the possibility of flooding rains eroding exposed banks. Persistent flooding scours a stream bottom, produces silt which smothers or washes away the insects upon which the ducks depend, and may mean that the stream, richer in soluble nutrients, carries less oxygen for future invertebrate colonizers.

The acclimation of numerous mammals in a land that originally had only bats and seals has been disastrous for some of the native avifauna of New Zealand. The deer, by removing some of the native cover and trampling the soil, have probably been responsible for much of the erosion. Rats, stoats, weasels, and polecats, plus the fairly plentiful wild cats, dogs, and pigs, all take eggs from ground nests and many prey on ducklings and incubating females. The introduction of insectivorous birds, which feed on the adult stages of the Blue Duck's invertebrate food, may also have effected the Blue Duck's decline. And finally, since the 1870's, trout introduced in most of the lowland streams have, we suggest, competed directly with the Blue Duck for food (Kear and Burton, 1971). Although such competition is still only conjectural, the birds live more commonly today on streams where the trout are scarce.

TABLE 1

Weights of Adult Blue Ducks*

| *Month* | *Males* | *Females* |
|---|---|---|
| February | 1075 | 850 |
| April | 800** | |
| May | 755 | 680** |
| July | 920**, 865** | 790**, 695** |
| December | 850**, 990**, 850** | 740** |
| Average | 890 | 750 |

*In grams.

**Captive birds.

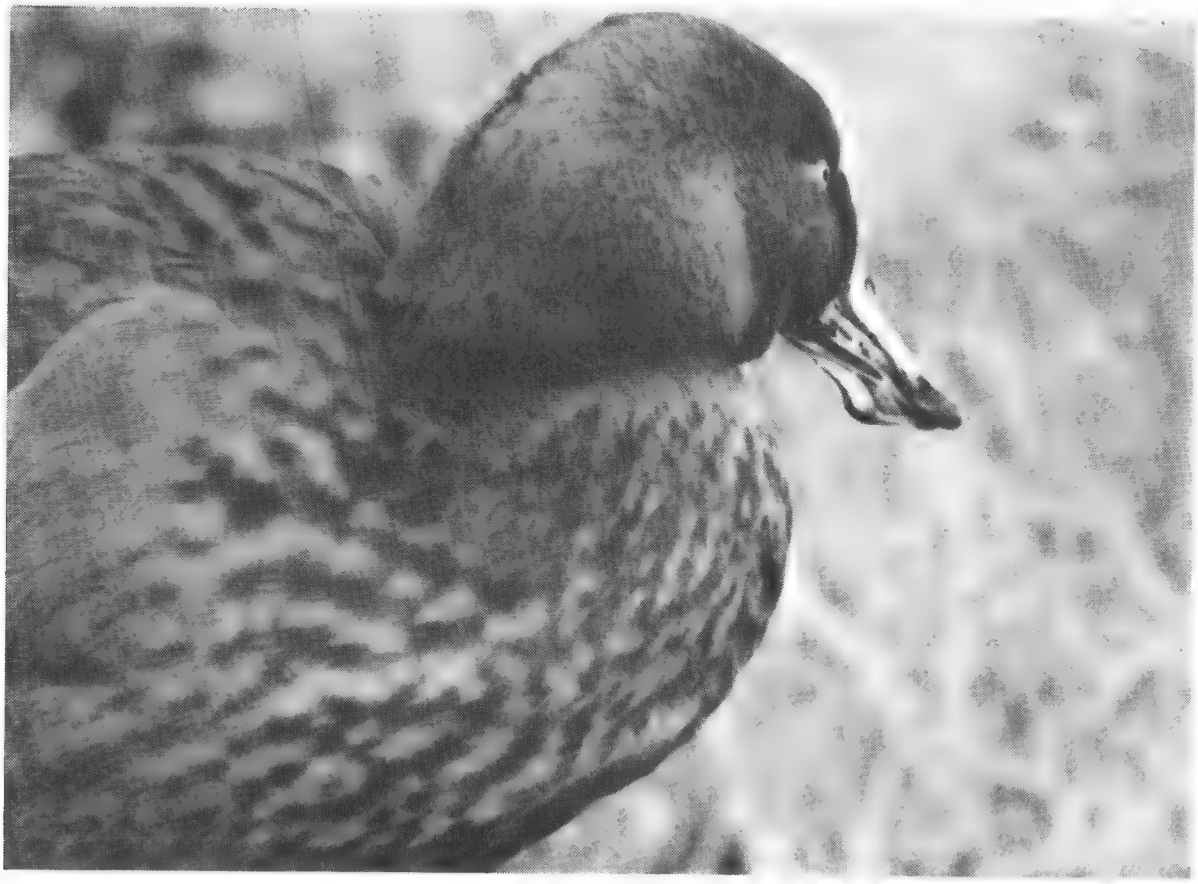


Figure 3. One of the most characteristic features of the Blue Duck is the bill, in which the lateral flaps of the upper bill may protect the jaw during the bird's active search among the stones of rocky stream bottoms for the aquatic insects that comprise the bulk of its diet. Photograph by Graham Byford.

## *Breeding Biology*

### Breeding Season

Male and female probably mate for life and defend their territory the year round. However, only preliminary studies of their social and sexual behavior have been made and there is no proof (Kear and Steel, 1971). Repeated copulations in the spring seem to maintain the pair-bond and perhaps serve to synchronize the reproductive states of the pair.

The breeding season extends over a long period — from August of one year to June of the next — suggesting that one pair may raise two broods a year (Travers, 1972). Guthrie-Smith (1927) supposed that the Blue Duck could begin nesting in August because the first broods appeared in September; and, indeed, Whitten (1972) reported a clutch of seven eggs, found north of Gisborne on 9 August 1971. We now have records of 20 nests with eggs, including two that I have seen; and we know the hatching dates for six of them (Table 2).

From observations of ducklings whose ages could be estimated, it was deduced that, for most broods, hatching occurs in October. However, the first broods probably appear in August (Figure 6). Blackburn (1960) saw a pair with young about three weeks old, near Gisborne, on 8 September. At the other end of the long season, ducklings are not unusual in February and March, and we have one record (T. H. Steel, pers. commun.) of five- or six-weeks-old ducklings on the Waipoa Stream on 10 April. The very latest record is of an adult with young, near Gisborne, on 10 June (Blackburn, 1956).

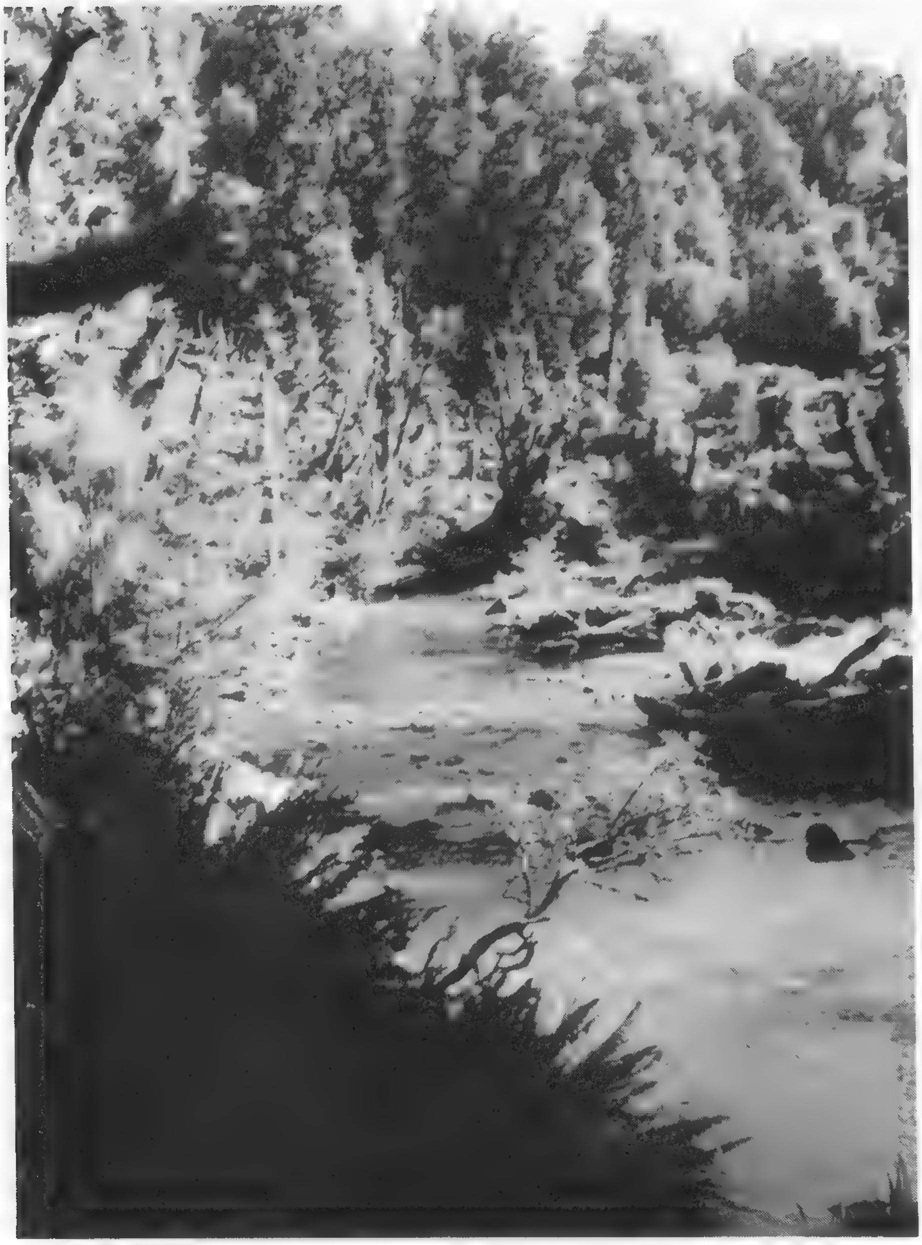


Figure 4. Typical habitat of the Blue Duck. The Waipoa Stream, North Island. Photograph by the author.

Many of these broods were in the North Island, and while there are not enough data to say that the breeding season varies according to latitude and altitude, it seems likely that, in the colder regions of the South Island and in the high mountains of both islands, Blue Ducks breed over a more limited period. The timing of egg-laying has probably evolved in relation to food supply. First, the female must have sufficient food to enable her to produce half her body weight in the form of eggs in about one week; and, second, six weeks later, the ducklings must have an abundance of food for growth. Because the food supply varies (Kear and Burton, 1971), it seems likely that a pair of Blue Ducks produces, on the average, only one brood a year. Nest-building, egg-laying, and incubation occupy 40 to 45 days, and the juveniles apparently stay with their parents until they attain mature plumage at the age of five months.

## Nest Site

The choice of nest site varies. In the wild, Blue Ducks select natural burrows (Figure 7). At Mount Bruce Native Bird Reserve, they used an artificial burrow. However, the species is by no means an obligate hole-nester (Potts, 1870; Buller, 1892). We have records of 18 sites: one each in a hollow log and hollow tree trunk; two each in rocky clefts in a bank, on ledges of rock on a cliff face, among the roots of a fallen tree, under logs overgrown by grass, beneath a bush of mountain flax, and under a *Carex* clump; and four under large clumps of tussock grass.

Normally, a canopy of vegetation prevents observation from above, as shown in a photograph by Howard (1963). The few exposed nests are relatively unaccessible as was the one on the cliff face, photographed by E. F. Stead (Oliver, 1955). Thus, the Blue Duck may select any site in the territory, usually well concealed but not necessarily so. Since three of the nests found in banks faced north, the sunny side, we may presume that the bird prefers warm, dry sites. There is no record of a Blue Duck nesting in an elevated tree site, such as the Astelia clumps favored by the New Zealand Grey Duck (*Anas superciliosa*), although Fulton (1908) stated that in North Canterbury Blue Ducks " . . . may be found nesting in trees."

Guthrie-Smith (1927) suggested that a pair may use the same site year after year, and this may well be true of successful sites. Since the recorded distances of Blue Ducks' nests from streams vary from a few feet to 30 yards, sudden rises in water level are a natural hazard. In the Urewera, one nest with eggs, only three and one-half feet above a stream, was undermined and washed away in December.

The nest itself is shallow and filled with any material within reach of the female. One nest contained leaves of the sedge *Uncinia,* grass, and leaves of Tawa, Mahoe, and Rimu trees, plus bits of ferns and moss and was lined with a quantity of gray-blue down which appeared to be less fluffy than the down in the nests of other ducks.

## Eggs

All the eggs seen were pale buff. A total of 48 (Schönwetter, 1960–1961; Oates, 1902; Canterbury and Wellington Museums; original) measured an average of 65.1 × 45.1 millimeters, with a range of 58.5–72.5 mm × 43.0–50.0 mm. Four eggs, taken by Guthrie-Smith (1927), had a mean weight of 70.5 grams; a calculated weight, based on the linear measurements of 12 eggs, was 73 gm (Schönwetter, 1960–1961). Although no unincubated eggs were weighed during the present study, the average size given above indicates that a fresh weight of 73 gm would be typical. Compared to the weight of the adult female, 750 gm (Table 1), the weight of a single egg is 9.7 per cent of the adult weight. Such a percentage is high for ducks in general — the egg of the Mallard (*Anas platyrhynchos*) represents 5.3 per cent of its body weight (Kear, 1965) and that of the Tufted Duck (*Aythya fuligula*) 6.7 per cent (Kear, 1970b). However, the relative size of the eggs is not unusual for New Zealand waterfowl. In the Brown Teal (*Anas aucklandica chlorotis*) the percentage is 10.5 and in the Scaup (*Aythya novaezeelandiae*) 9.0 per cent (Lack, 1968).

## Clutch Size

The meager information on the clutch size, shown in Table 3, is based on 13 nests either found in the wild and in museum collections or reported in the literature. The mean clutch size is 5.4 eggs and the most frequently occurring number is five. Oliver (1955) gave a clutch-size range of four to nine; Guthrie-Smith (1927) reported broods of nine young; and Mr. H. R. Roberts

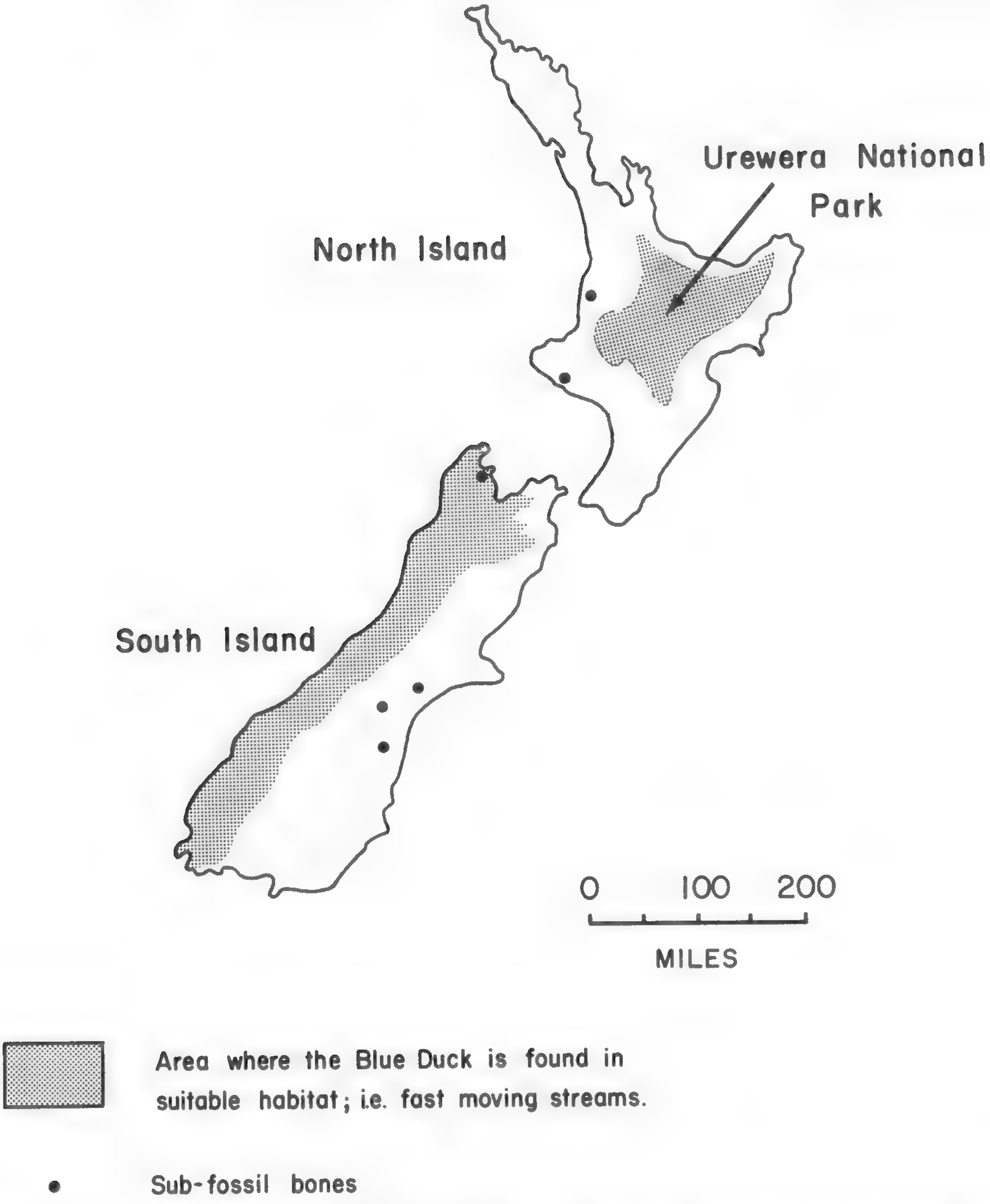

Urewera National Park
North Island
South Island
0 100 200
MILES
▨ Area where the Blue Duck is found in suitable habitat; i.e. fast moving streams.
● Sub-fossil bones

Figure 5. The distribution of the Blue Duck in New Zealand. The areas, indicated by cross-hatching, show where the birds occur today — always in forests cut by fast-moving streams. The dark squares pinpoint sites where sub-fossil bones of the Blue Duck have been found. Note that there is only one dot within the present area of distribution.

(pers. commun.) told me of one unusual brood with 10 ducklings. However, most broods number only three, four, or five. Five eggs is a small clutch for a dabbling duck — the Mallard lays 10 or 11 eggs on the average — but just as New Zealand waterfowl tend to lay larger eggs, they also tend to produce fewer of them. The average clutch of the Brown Teal is 6.0 eggs and that of the Scaup 5.4.

The relatively small clutch size in these birds may reflect a low rate of predation. Many pressures, such as large food stores necessary for egg development, the time needed to lay a given number, and the greater ease of incubating fewer eggs, may favor a small clutch in any species. However, a small clutch is an advantage only when predator pressure is also low and enough young will survive. On the other hand, larger eggs might make the smaller number necessary. Lack (1968) suggested that there may be a selection for larger eggs because the ducklings, if heavier at hatching, have a better chance of surviving should feeding conditions be unfavorable.

### Incubation Period

Eggs, collected and incubated artificially during the present study, hatched in 31 and 32 days, the last of the four ducklings appearing 36 hours after the first. Mr. C. R. Roderick (pers. commun.) thought that the incubation period of eggs, hatched by birds in captivity at the Mount Bruce Native Bird Reserve, was 31 days. The majority of dabbling ducks, the Anatini, hatch in 25 to 28 days (Lack, 1968). Within this group the only incubation period comparable in length to the period of the Blue Duck is that of the Bronze-winged Duck (*Anas specularis*), a South American dabbling duck.

TABLE 2

Records of Blue Duck Nests with Eggs

| *Month* | *Number of nests* | *Hatching dates* |
|---|---|---|
| August | 1 | |
| September | 1 | |
| October | 7 | 13, 17, 18 |
| November | 8 | 8, 15 |
| December | 1 | 24 |
| January | 2 | |

Only the female incubates. She leaves the nest to feed, drink, and bathe probably in the early morning and certainly just before darkness falls in the evening. The male accompanies her while she rapidly searches the shallow water for food, and they call softly to one another most of the time. After about 45 minutes, he escorts her back to the nest. It is at this time that one finds the nest most easily; the birds, if unaware of the human observer, simply lead one to it. The drake spends the night some distance away from the nest on a boulder in the middle of the river. During the day, he is hidden beneath an overhanging bank or a log (Steel, 1970; Kear and Steel, 1971), and the only indications of his presence on the territory at this time are gritty brown droppings splashed on the rocks.

### Young

As I already noted, hatching commonly occurs in October and November (Figure 6). According to Steel (pers. commun.) one brood remained in the nest for 43 hours before traveling to the stream in the early morning. During that period, the male visited the nest frequently and was present when they went to the water. Unlike many duck species (Kear, 1970a), the Blue Duck male shares in the care of the young. However, the ducklings' food and anti-predator displays, inconspicuous in both parents, are apparently unnecessary (Kear and Steel, 1971).

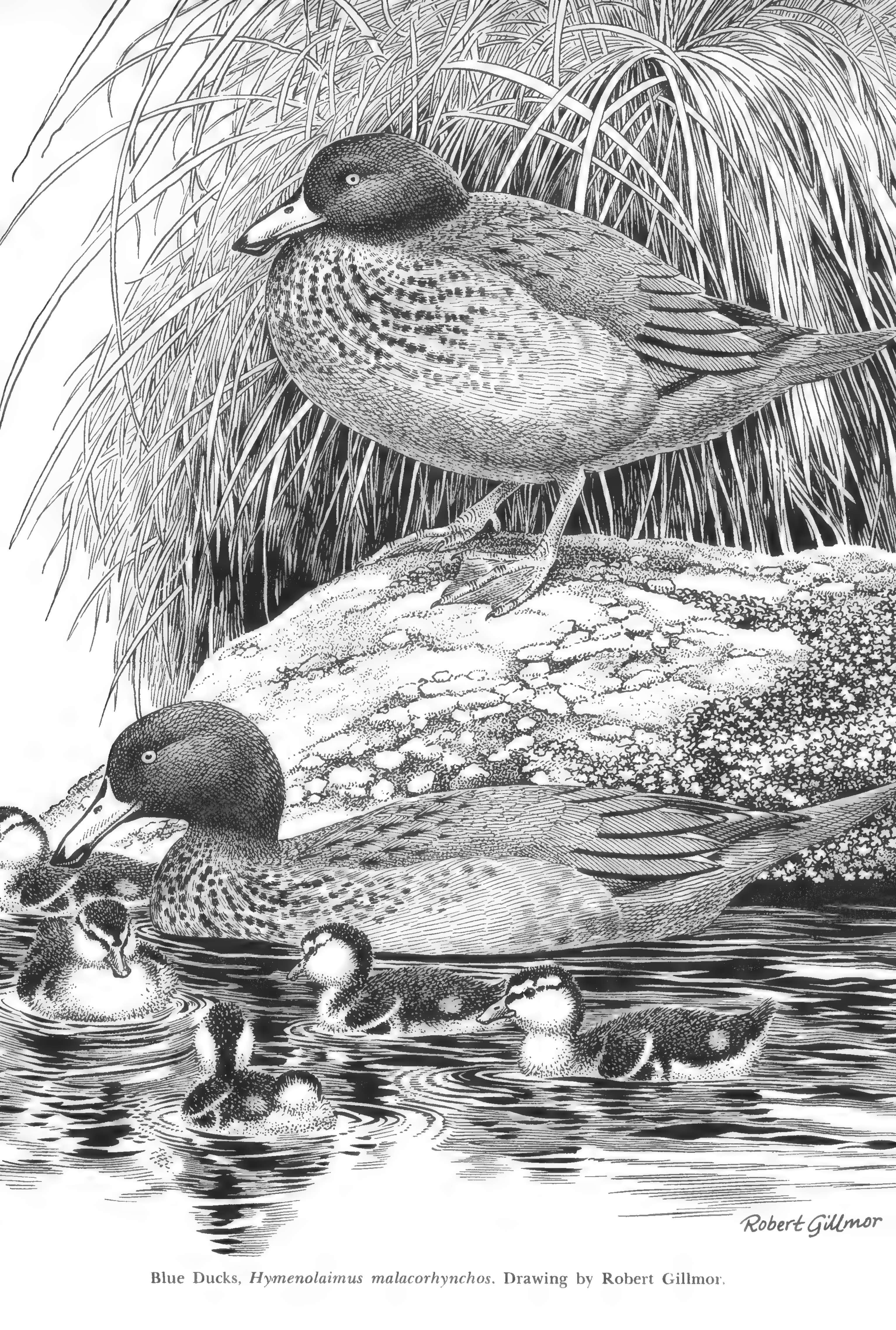
At hatching, the four captive ducklings averaged 45.5 gm, some 14 gm more than newly hatched Mallards. A peculiarity of the Blue Duck is a suggested sex-linked color difference in the spotting on the back which is chestnut in male ducklings and fawn-colored in females (Pengelly and Kear, 1970). We do not understand the significance of the difference and consider it quite surprising since in coloration the sexes of the adults are indistinguishable.

The ducklings' development in feathering, weight, and bill length was slower than that in species breeding at higher latitudes. The ducklings did not acquire their full juvenal plumage until they were eight weeks old and took their first flights when between 10 and 11 weeks old (Pengelly and Kear, 1970), a fledging period that is long even for ducks of the warm temperate regions (Lack, 1968, Appendix 16). Lack's suggestion (1968) that, in many birds, the fledging period is strongly correlated with the length of the incubation period seems to be true in the Blue Duck.

The young Blue Ducks stayed in the rather dull gray and brown juvenal plumage until they were five months old. Even then, some signs of immaturity remained. The bill changed more gradually from light blue to white, and the eyes from dark brown to golden yellow. The young birds seem to stay in the territory of the parents. We do not know how the family eventually breaks up. Possibly the adults chase away the young when they attain a mature plumage, and thus appear to be potential rivals.

Where the young birds go, how far they migrate, and how they find mates and territories of their own are still unanswered questions. Their long-range flying ability is probably good, but being tame they appear reluctant to take off. Once on the wing they are strong, swift flyers. The wing-beats of the adults were timed from motion picture film at eight completed strokes per second, or 480 per minute. This is faster than the 300 per minute obtained by Meinertzhagen (1955) for several *Anas* ducks, but slower than the 12 beats per second recorded by Johnsgard (1966) for the Torrent Duck (*Merganetta armata*).

The slow growth rate and the lengthy period of parental care, which probably evolved in relation to a limited amount of available food, have a selective advantage in that the species is able to make wide use of the available habitat. However, the slower growth means that the young are helpless and subject to predation over a longer period. In the Blue Duck, the relatively slow development presumably also evolved in association with a general lack of predators in New Zealand. The flightless ground rails (*Gallirallus*), now much reduced in range, may have taken a few eggs in the past. The Bush Hawk (*Falco novaeseelandiae*), Harrier (*Circus approximans*), and some of the gulls (*Larus*) may prey on very young birds. And circumstantial evidence suggests that the larger eels occasionally feast on ducklings. The white belly and dark upper parts of the ducklings could indicate some necessity for camouflage from beneath, but the significance of the downy plumage pattern is obscure. In view of the supposed low level of predation, it is also puzzling that both the juvenal and adult plumages are so cryptic and that the birds are very difficult to spot until they call — which they almost always do.


Robert Gillmor

Blue Ducks, *Hymenolaimus malacorhynchos*. Drawing by Robert Gillmor.

Slow development imposes certain restrictions on a species rearing its young in such a hazardous place as a mountain torrent. Although the ducklings usually come to little harm when moving downstream with the current, they sometimes have to go ashore and walk back to the top of the territory again. Until they are well grown and can fly, leading them and keeping them together in swift water and on the steep banks may be the principal value of dual parental care. Occasionally, ducklings are swept away over waterfalls, and for this reason and various others, the size of the broods declines with age.

I determined the diet of the ducklings only from an analysis of two samples of droppings. Three-day-old ducklings ate caddis fly larvae, stone fly and mayfly nymphs, and chironomid larvae. We also found parts of an adult fly, an adult beetle, and a mite (Kear and Burton, 1971). The droppings from 14-day-old ducklings contained similar items with a greater proportion of caddis flies, especially the species *Olinga,* the larvae of which inhabit a horny case.

Since ducklings need food more often than adult birds, a typical family party consists of offspring bobbing and dipping beneath the water and dashing across the surface while their parents float placidly nearby. The adults' feeding activity is greatest in the early morning and late afternoon. Their summer diet, all that we have investigated so far (Kear and Burton, 1971), consists of both case-living and free-living caddis fly larvae, other aquatic nymphs, and algae, and, for a short time, caddis fly pupae. This diet must change with the seasons because, so far as we know, all New Zealand caddis flies, except *Olinga,* take a year to complete their cycle and the larvae are more plentiful, though smaller, in mid-summer than in winter.

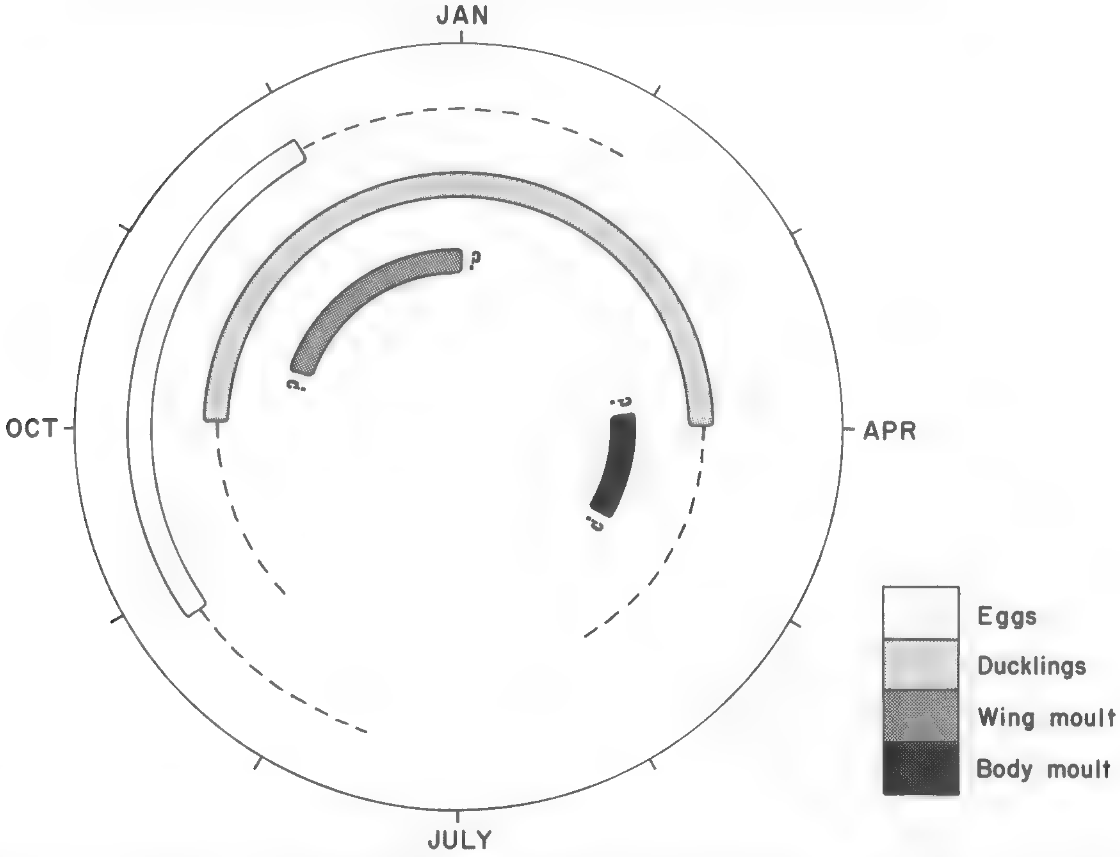


Figure 6. The annual cycle of the Blue Duck. The white bar shows eggs; the light gray, ducklings; the dark gray, wing molt; and the black, body molt. The dotted extensions are the extremes. Question marks beside the dark gray and black bars mean that the timing is only conjectural.

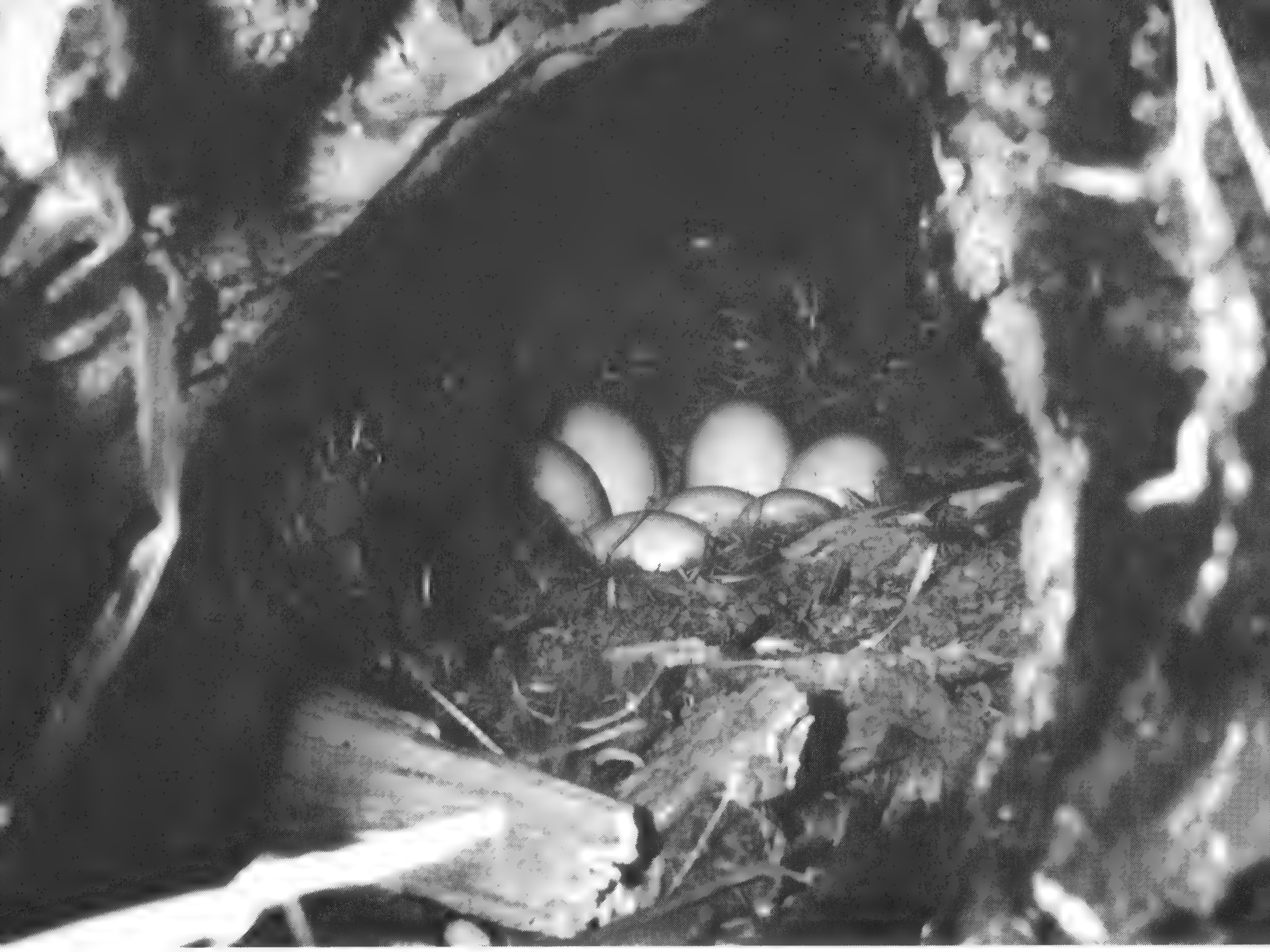


Figure 7. The Blue Duck usually nests in natural cavities, often in a tree as shown here, but sometimes in a hollow log, on ledges of rocky cliffs, beneath bushes, in shallow cavities in banks, among the roots of a fallen tree, and under large clumps of tussock grass. Photograph by A. J. Whitten.

## *Molt*

The time of the wing molt in breeding birds is uncertain. There are no records of broods with flightless parents. In captivity, at Mount Bruce, the unsuccessful breeders dropped their primaries in late November and could fly again by mid-December (Figure 6), the female of the pair beginning her molt before the male. At Slimbridge, England, an unmated captive drake molted in early July, roughly the equivalent of January in New Zealand. At Gisborne, New Zealand, a captive female was in full wing molt when she died in May, indicating that the species can lose its feathers at almost any time although this bird's molt may not have been normal. We know even less about the timing of the second body molt which is common to all ducks (Delacour, 1956) and during which many species assume breeding plumage. The only evidence of this was in an adult male which acquired new contour feathers in February while still retaining his flight feathers.

Changes in body weight throughout the year are probably normal once the bird is mature. For the moment there are too few data for definite statements. Table 1 lists the weights of 13 captive or wild Blue Ducks.

## *Taxonomic Relationships*

The taxonomic position of the Blue Duck is clouded. Delacour and Mayr (1945) suggested that the species might be an aberrant *Anas*. Delacour (1956) placed it tentatively with the dabbling ducks (Anatini) and Johnsgard (1965) followed this classification. There is now additional information on a number of characters.

For instance, the bony bulla of the male's syrinx is asymmetrical (Figure 8). Also, the Blue Duck has a tracheal tube of uniform diameter and a bulla that is evenly ossified and spherical in shape. Its general configuration resembles that of many dabbling ducks (Anatini), perching ducks (Cairinini, including the Torrent Duck, *Merganetta*), shelducks (Tadornini), and even eiders (*Somateria*) and the Harlequin Duck (*Histrionicus histrionicus*) according to Johnsgard (1961), but is particularly like the bulla of the Chiloe Widgeon (*Anas sibilatrix*) and North American Wood Duck (*Aix sponsa*). The bulla is larger and not as left-sided as that of Hartlaub's Duck (*Pteronetta*, a perching duck, sometimes called *Cairina hartlaubi*), nor as oval as that of the African Black Duck (*Anas sparsa*). The large size of the bulla is probably correlated with the very strong territorial whistle of the male.

TABLE 3

Clutch Size of the Blue Duck

| | | | | | |
|---|---|---|---|---|---|
| Number of nests | 2 | 7 | 2 | 1 | 1 |
| Number of eggs | 4 | 5 | 6 | 7 | 8 |

The simple voice of the duckling, especially the distress call, provides taxonomic clues (Kear, 1968) since, at this age, related species usually sound alike and unrelated ones do not. Figure 4 shows a sonogram tracing of the cry of an isolated duckling. The shape of the individual note is not unlike that of Hartlaub's Duck; it is also like that of the Mallard and a number of similar dabbling ducks such as the Yellow-billed Duck (*Anas undulata*), Grey Duck (*A. superciliosa*), Chestnut Teal (*A. castanea*), and even the Bronze-winged Duck (*A. specularis*) and the Crested Duck (*Lophonetta* = *A. specularioides*). The rate of performance is slow, the call being rendered at about three notes per second. The Yellow-billed Duck (*A. undulata*) and Mallard (*A. platyrhynchos*) have four; the Bronze-winged Duck (*A. specularis*) and Grey Duck (*A. superciliosa*) have five; the Chestnut Teal (*A. castanea*) and Hartlaub's Duck (*Pteronetta*) have six; and the Crested Duck (*Lophonetta*) has six and a half. The note of the Blue Duck chick (Figure 9), resonated at just below four kilocycles per second, is slightly lower than the *Anas* species listed above. But only the shape of the note is considered significant in classification (Kear, 1968); the size of the duckling probably determines the speed and frequency, at least within any group such as the dabbling ducks.

In color the Blue Duck downy young are unusual: black, white, and ginger, with the black suffused with a metallic green sheen (Pengelly and Kear, 1970). In patterning, however, they resemble the young of other dabbling and perching ducks, and they do have the typical dorsal spotting despite statements to the contrary (Delacour, 1956; Johnsgard, 1965). The vertical dark stripe running from the eye to the crown is unusual, being found in the downy young of only two other species — the Torrent Duck (*Merganetta*) and the Black-headed Duck (*Heteronetta atricapilla*).

The Blue Duck's virtual lack of a wing speculum and the presence of the black edging on the innermost secondaries are unique features among the Anatini. But, as Johnsgard (1965) pointed out, black margins also occur on two similar feathers on the wing of *Pteronetta* where there is no speculum at all — not even the white border found in the Blue Duck. The black lines may assist in the imprinting of young on their parents since such lines would be particularly conspicuous to a duckling following an adult. No one has investigated this as yet.

The Blue Duck's social behavior again shows similarities to different duck groups. Its preflight signal is more like the Chin-lifting of *Tadorna, Pteronetta,* and some *Aythya* than the Neck-jerking and Head-shaking of most dabbling ducks (Kear and Steel, 1971). Its system of shared parental care seems to be a "primitive" feature in waterfowl that does not occur in diving ducks but is present in a few Anatini and Cairini such as *Anas specularis, A. sparsa, A. sibilatrix, Merganetta,* and *Pteronetta* (Kear, 1970a). The Blue Ducks give Head-bobbing, as is typical of all dabbling ducks, in the precopulatory situation with occasionally an intense bathing display by the female, perhaps like that described by Johnsgard (1965) for *Anas sparsa.* The male may touch the female on the back, as in *Aix sponsa* and *Anas sparsa,* yet after copulation he does not Bridle or Nod-swim as do most *Anas* males, but merely assumes a slightly erect posture not typical of any other species (Kear and Steel, 1971).

Biochemical studies sometimes reveal evolutionary relationships. However, in the case of the Blue Duck, Mr. A. H. Brush (pers. commun.) found the electrophoretic profiles of its feather proteins unique and unlike those in any other dabbling duck, all of which tend to be rather similar. On the other hand, Miss S. A. Stewart (pers. commun.), in a preliminary analysis of egg-white proteins, finds the Blue Duck closer to *Anas specularis* than to *A. platyrhynchos, Aythya,* or *Aix,* and only more distantly related to *Tadorna.*

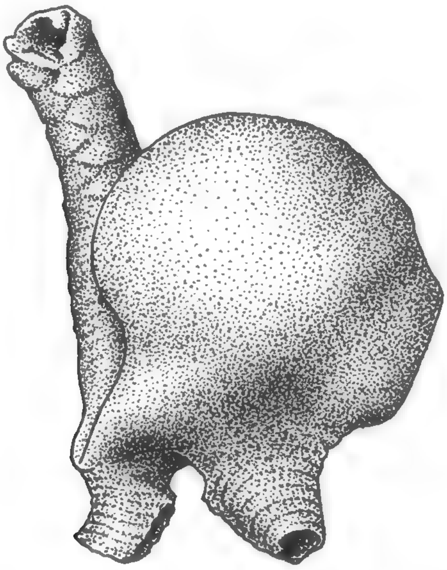


Figure 8. The trachael bulla of the Blue Duck. Note that it is spherical and asymetrical. For comparison with those in other ducks, see Johnsgard (1961).

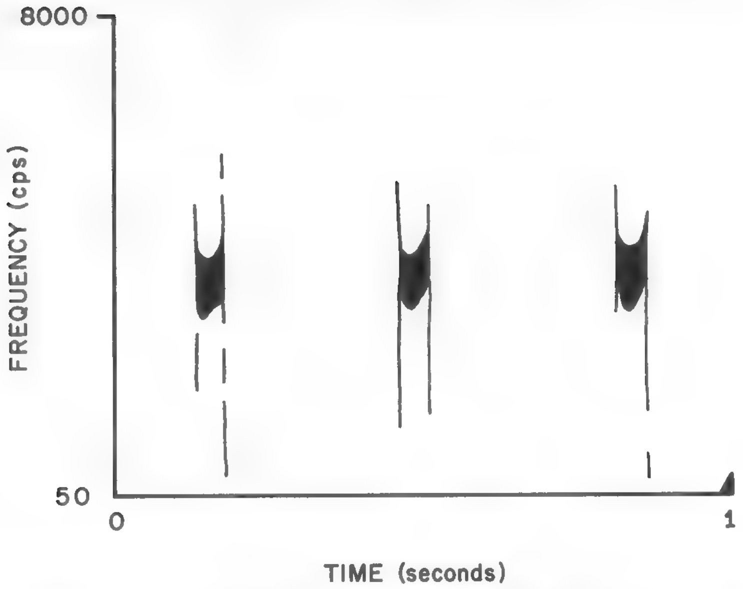


Figure 9. A sonogram tracing of the distress call of a young Blue Duck. Time on the horizontal scale equals one second; frequency on the vertical scale is 50–8,000 cycles per second. For comparison with the calls of other young ducks, see Kear (1968).

For the moment we should best think of the Blue Duck as deriving from an early stage in the evolution of the dabbling ducks from their perching, duck-like ancestors. It shows, perhaps, the greatest similarity to *Pteronetta* and *Anas sparsa* — respectively considered by Johnsgard (1965) as a possible link between perching and dabbling ducks and the most generalized *Anas* — although in a number of features it is different from both those species.

A banded population could provide excellent opportunity for studies of longevity, faithfulness to a particular mate, the possibility of double broods, and year-round defense of territory. Even though the population is small, one might investigate the significance of territory and test a number of hypotheses by manipulating its size or the food supply. The bird itself is so tame and easily caught, and the territory boundaries so clearly marked that the inconvenience of a remote study area might not be a disadvantage. Probably the security of this unique bird depends on the inaccessibility of its habitat.

## *Summary*

I have reviewed the breeding biology of the Blue Duck (*Hymenolaimus malacorhynchos*), a species that has decreased in numbers over the last century and is now limited to remote mountain streams in New Zealand. The most important factors contributing to its decline include habitat destruction and the introduction of predators and possible food competitors.

Nesting occurs mostly in September, October, and November, but the breeding season extends over more than half the year. While the choice of nest site varies, it is most frequently in a river bank and well hidden. As in many New Zealand ducks, the egg, at 73 gm, is relatively large and the clutch of five relatively small. The female alone incubates for 31 to 32 days and the ducklings' growth is slow. They do not fly until they are about 10 weeks old.

A discussion of the species' taxonomic relationship, with reference to the tracheal bulla, plumage characters, duckling voice and pattern, and social display, leads to the conclusion that the Blue Duck shows affinities with the perching ducks (Cairini) and the dabbling ducks (Anatini) and, for the moment, belongs with the dabbling ducks.

*Acknowledgments*

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# FOOD REQUIREMENTS AND GROWTH OF CATTLE EGRETS IN SOUTH AFRICA

W. Roy Siegfried

In recent years, the Cattle Egret (*Ardeola ibis = Bubulcus ibis*) has undergone a remarkable expansion in range. Skead (1952) and Siegfried (1965, 1966a) documented the bird's spread in South Africa. In addition, Siegfried (1971c) reported on the Cattle Egret's rate of population build-up in relation to the species' reproductive output and mortality.

In the southwestern Cape Province and in other man-modified regions of South Africa, the Cattle Egret normally produces clutches of three or four eggs, but usually rears successfully only two chicks out of broods of three or four young. Starvation, the major cause of chick mortality, is heaviest when the chicks are around 10 days of age (Siegfried, 1972a).

The present paper reports on the growth and food requirements of Cattle Egret chicks during the nestling period, examining these aspects in relation to the food-gathering capacity of the parents. I have already discussed the development of plumage and the molt succession (Siegfried, 1971b).

I made the study during three years, 1965–1967, in a heronry near the town of Paarl, 33° 43′ S Lat., 18° 55′ E Long., in the southwestern Cape Province, South Africa. A general description of the heronry and its man-modified environs can be found in Blaker (1969) and Siegfried (1972a). The heronry normally contains some 8,000 Cattle Egrets nesting in trees.

## *Food Requirements and Growth of Chicks*

Twenty-eight Cattle Egret chicks, between 12 and 24 hours old and dry, weighed from 21 to 26 grams with a mean weight of 23.7 gm. Each chick was the first of its brood to hatch.

Figures 1 and 2 illustrate the rate of weight increase and the food consumption of artificially reared chicks. The chicks, weighed before and after each feeding, were given mainly minced lean beef (73 per cent water and 6.04 kilocalories per gram) and a multi-vitamin supplement, and were fed as much as they could eat at least three times a day.

The graphs in Figure 1 show that the chicks' weight increased relatively rapidly during the first two weeks when they gained about 70 per cent of their total growth. The peak growth rate, with weight added per day, occurred at

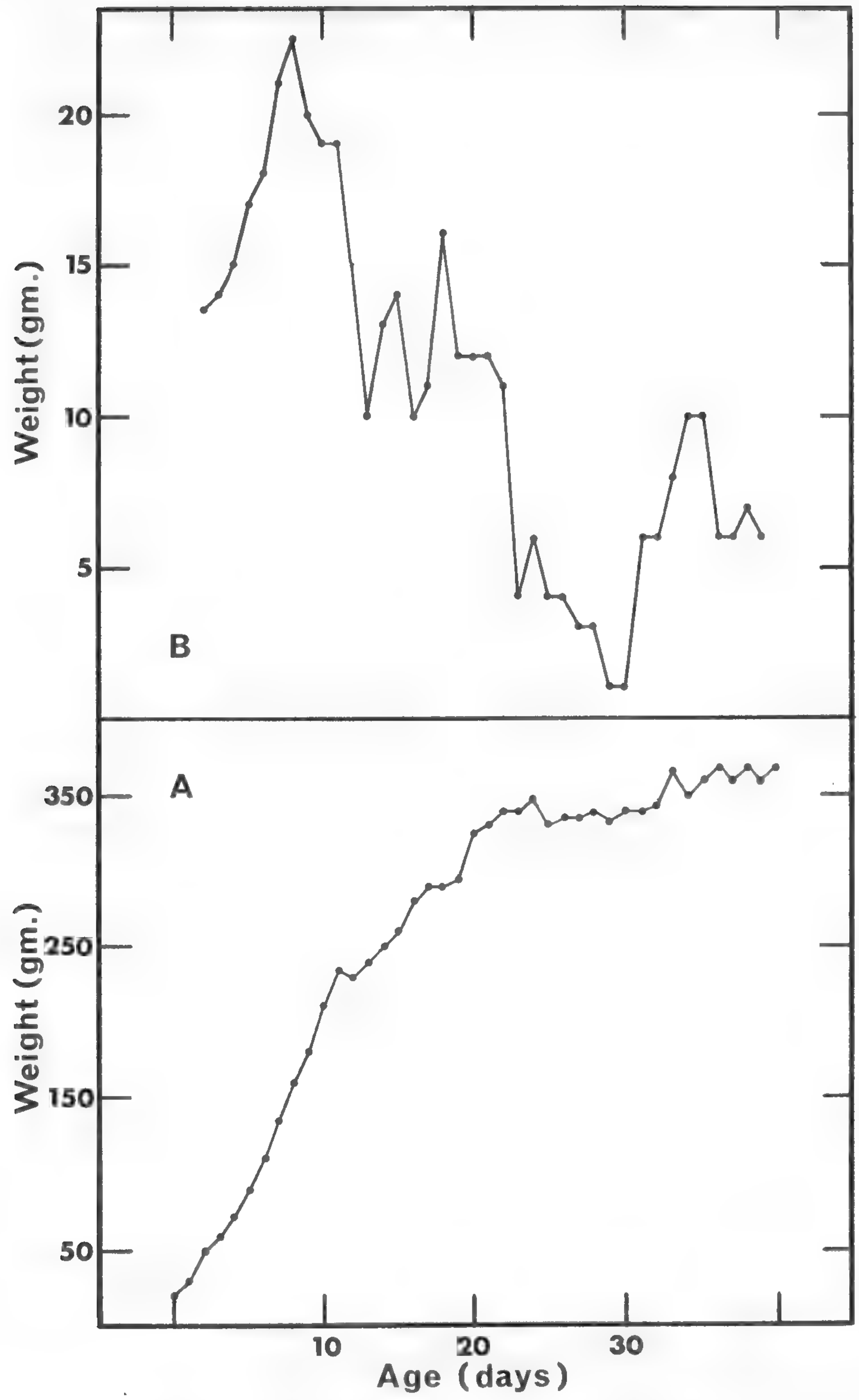

Figure 1. Mean daily growth in body weight (A) and growth increments (B) of three Cattle Egrets. B is plotted as moving averages of five.

about the age of one week. At this age daily consumption of food, weighed fresh, was about 75 per cent of a chick's body weight. The greatest daily food consumption occurred when the chicks were about two weeks old. After that, the rate of increase in body weight slowed down and when they were three weeks old, it began to level off.

I estimated that a chick, in growing from one to 21 days, requires an amount of energy equal to that contained in 1,676 gm of suitable insect food, weighed fresh. The chick takes approximately 40 per cent of this during its second week of life when it requires an average of 95 gm daily. In converting beef-intake to insect-intake, I assumed a mean caloric value of 5.5 kcal per gm and a water content of 70 per cent as being representative of a Cattle Egret's insect food (Siegfried, 1969).

Developing young birds require energy for growth and maintenance. In altricial species, these requirements are proportional to their weight and rate of growth. We must also consider the thermodynamics as long as the chicks remain in the nest. In larger broods, each individual chick, by huddling with its nest mates, requires less energy to maintain its body temperature than the single chick alone in a nest (Royama, 1966). Maximum specific energy for growth comes when the young are about half grown; at this time the amount of energy needed for maintenance is about half that required later by fully grown birds. In actively growing young the combined energy demands may exceed the maintenance requirement of fully grown young (Dawson and Evans, 1957; 1960).

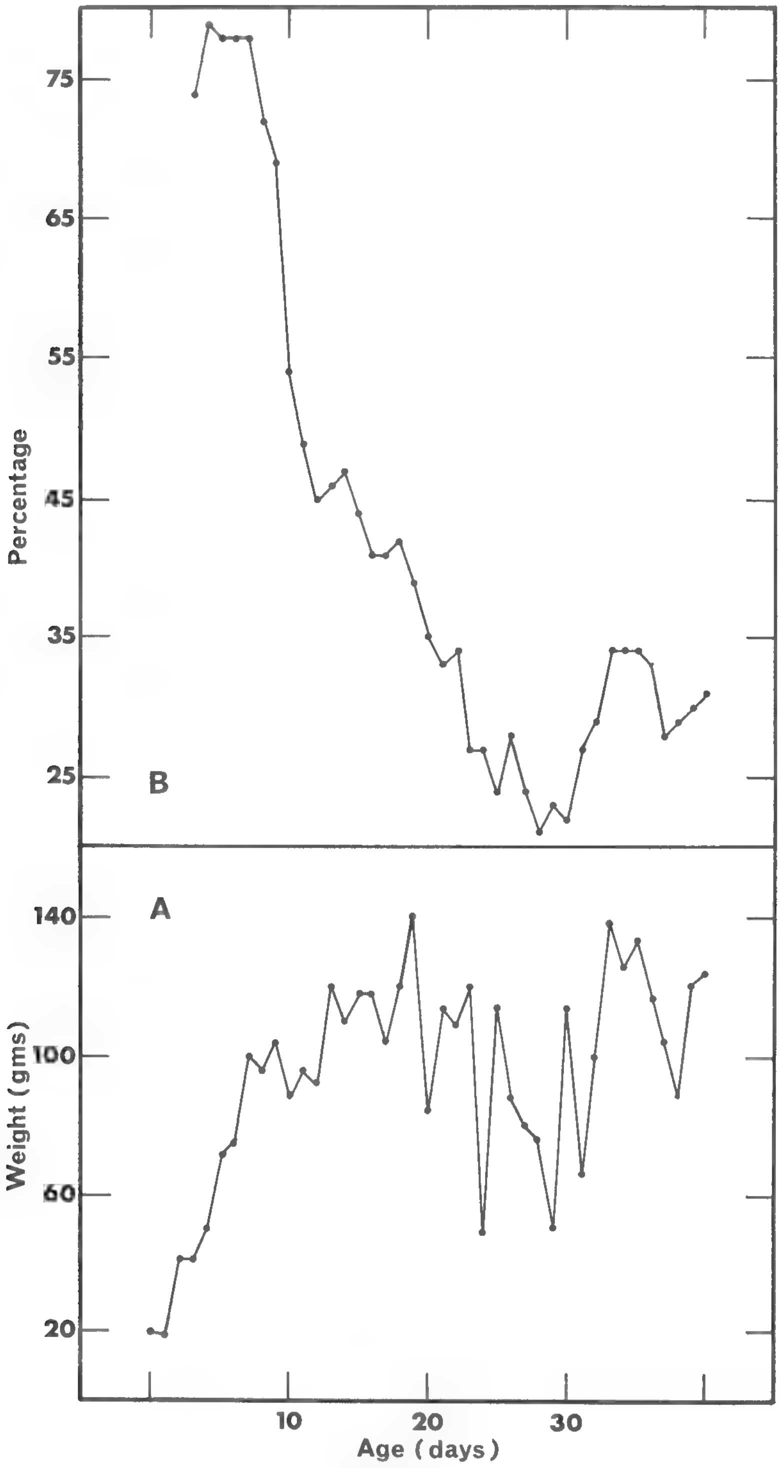

Figure 2. Mean daily food consumption (A) and relative food consumption (B) of three Cattle Egrets. B is plotted as moving averages of three.

$$\text{Relative food consumption} = \frac{\text{per cent mean daily food}}{\text{per cent mean daily weight}}$$

Since the rate of energy consumption is directly proportional to the amount of foodstuffs oxidized and the amount of water lost during respiration, I estimated the metabolic rates of Cattle Egret chicks by measuring the chicks' loss in weight when they were not fed. The actual procedure that I followed in making the measurements involved moving the chicks, in the morning immediately after they had been fed, from their nests to individual wire-netting cages in a temporary field room with a constant air temperature where I weighed them at regular intervals. The graph in Figure 3 traces the weight-loss in relation to the age of the chick. It appears that the energy requirements were highest during the end of the second week after hatching, when feather growth, a process that presumably demands much energy, reached its maximum.

Figures 4–6 summarize data gathered on the growth rates of Cattle Egret siblings during the middle of the breeding season when breeding success was best (Siegfried, 1972a). I obtained the data from successful broods only, recording the average growth rates of chicks from broods in which all chicks fledged, and then plotted the data according to the actual ages of the chicks. For example, in Figure 5 the weights given for each triplet on the fifth day are not the weights recorded on the fifth day of nest inspection, but refer to the weight of each individual chick when it was five days old. Consequently, the differences in size and weight between siblings that hatched at different times, when measured at the same time on the same day, were even greater than indicated in Figure 5. Because chicks older than about two weeks are difficult to capture, scrambling out of the nest and fleeing from approaching humans, I secured the individuals, whose weights I monitored daily, to their nests by a ribbon attached to the leg.

A number of salient features emerge from Figures 4–6. The average growth rates of the chicks that hatched first and second in twin and triplet broods are nearly identical and equal to the growth rate of single chicks. I have no evidence that the biggest chicks in broods of two and three grew faster than the single nestling as, for example, in the Lesser Black-backed Gull, *Larus fuscus* (Harris, 1964).

The Cattle Egret that hatches last in a brood of three grows more slowly than its siblings and remains retarded throughout the entire nestling phase. At five days of age, the growth rate of the last-hatched chick in broods of three shows the beginnings of a marked departure from the growth rate of its siblings, becoming slower. This reduction in growth rate occurs at a time when its older siblings change from peck-feeding to grab-feeding, which I shall discuss below. The divergence between the last-hatched chick and the older siblings is relatively greatest when the chick is about 10 days old, coinciding with the peak in the energy requirement of the brood.

Thereafter, the growth of the third-hatched chick, if it survives, catches up a little on its older siblings, but still remains slightly slower. These findings support the conclusion, reached elsewhere (Siegfried, 1972a), that in broods of three, the chicks that succumb through starvation are invariably the last hatched; and that inadequate nutrition is the main factor responsible for the relatively high mortality of chicks from one to two weeks old. The chick's second week of life is, therefore, the critical period. If the chick survives into the third week, then its chances of remaining alive for the rest of the chick phase improve. Although the daily absolute energy requirement of the brood may occasionally increase after two weeks, the overall relative growth rate

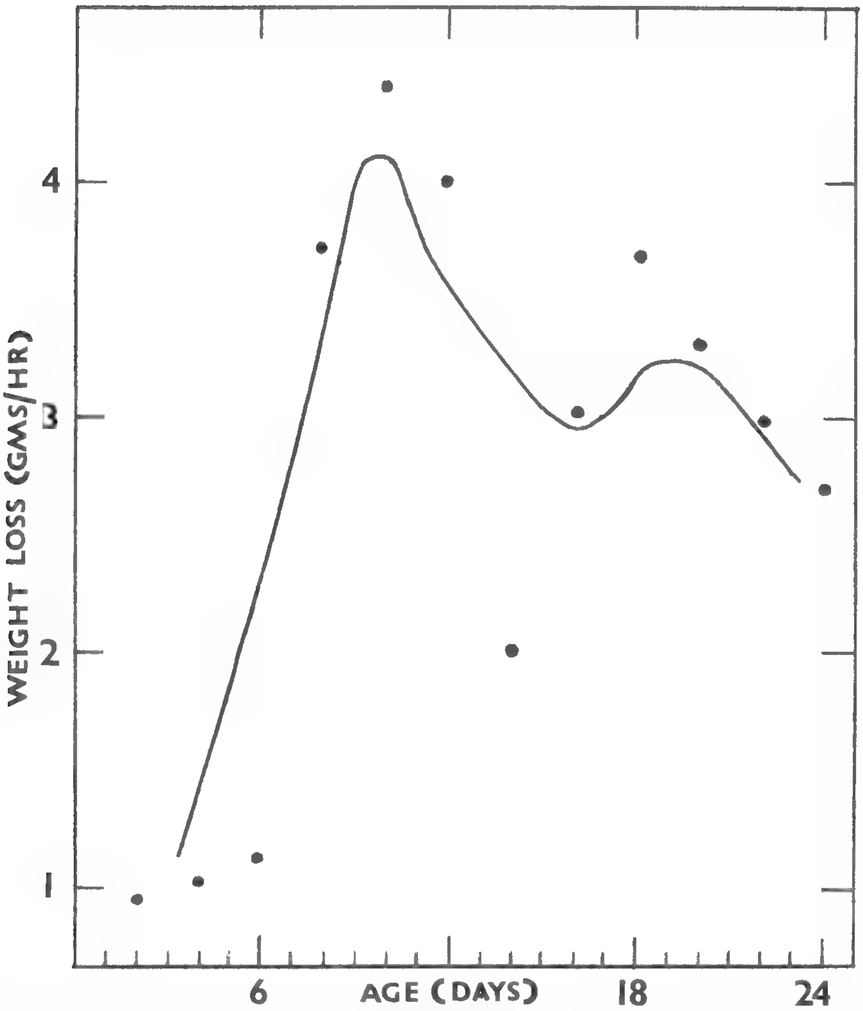

Figure 3. Mean weight loss in nestling Cattle Egrets at ambient temperature of 25° C. Data from two chicks for each age group and the largest chick from each brood.

and relative food consumption decline as well as the percentage of food used for tissue growth. As a result, the older chicks in a brood survive a temporary food shortage better than the younger ones.

The figures given in Table 1 support to a certain extent — though the data are rather meager — the fact that the increased failure of broods toward the end of the breeding season is due to retarded development and starvation of the entire brood (Siegfried, 1972a). The figures also suggest that growth rate in first-hatched chicks, hatched late in the season, may be slower than in first-hatched chicks hatched early in the season. It is important to note that the weights in Table 1 are only of chicks which eventually fledged.

## *Behavior of Parents and Chicks*

Blaker (1969) provides some information on the behavior of the chicks of the Cattle Egret and their parents during hatching and rearing.

In clutches of more than one egg the siblings hatch at different times, asynchronously; the egg laid first hatches first. Normally, as soon as the brooding and guarding by the parents cease — about two weeks after hatching, but often earlier — the chicks wander increasingly from the nest. By the time they are four weeks old, they spend most of the day perched on branches in the treetops above their nests, returning to the nests only to be fed. They are entirely dependent on their parents for food until they are six weeks old. We refer to chicks between three and six weeks old as "branchers" (Siegfried,

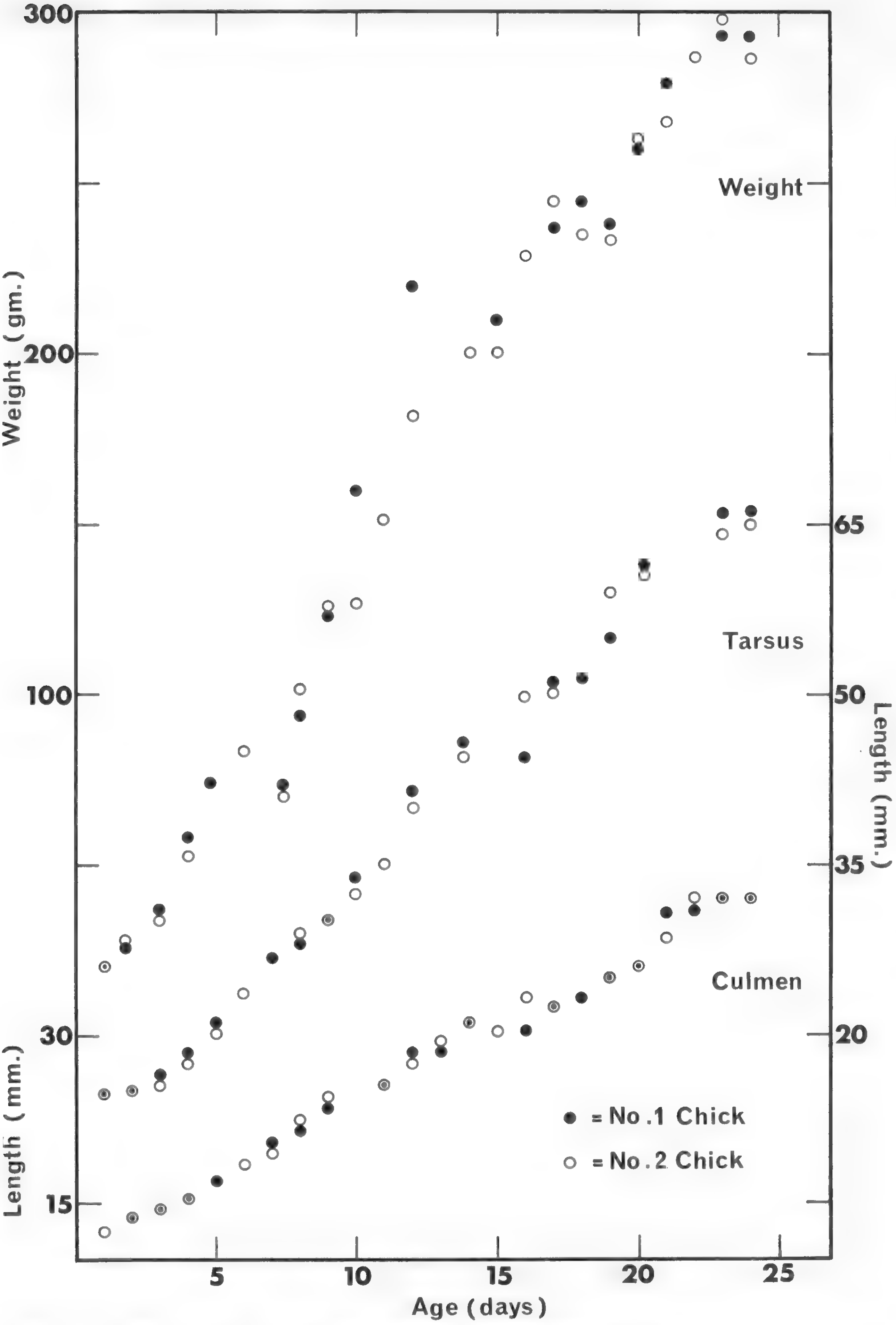

Figure 4. Mean growth curves of body weight, tarsus, and culmen for individual Cattle Egret chicks in a brood of twins. Data from 12 different broods.

1966b). Thus, chicks are "nestlings proper" during the first three weeks of life and branchers for the next three weeks, after which they fly strongly.

During the first week of life, the chicks get most of their food by pecking from the nest the food boluses deposited there by the parents. After the first week they obtain food directly from the parent by grabbing its bill. Captive chicks, reared artificially, show the same transition from food-pecking to food-grabbing at the same age. Up to one week, the chicks picked up food from the floor of the cage; after one week they only ate food placed directly in their bills. This change in feeding method has important implications affecting the chick's rate of growth and survival.

Coincident with the onset of maximum energy demand — at two weeks — a number of significant behavioral changes occur in parents and young. The parents cease guarding the young; thus, both adults are able to forage at the same time, increasing the amount of food brought to the nest. Second, the parents react aggressively to strange young placed in the nest whereas, up to this time, they would have accepted them. The young, in turn, perfect a threat behavior, defending both the nest and themselves more effectively. At the same time, they begin to leave the nest more readily when approached by humans.

Data published by Blaker (1969) suggested that Cattle Egrets with large broods cease guarding their young earlier than parents with smaller broods. If this is so, the compromise must be delicately balanced between the chances of promoting the survival of the young by providing more food, through both parents foraging, and the chances of promoting the survival of the young by providing the protection of one parent on the nest. The young need protection against actual predators and against conspecific members of the heronry which sometimes take over and dismantle a nest. Night Herons (*Nycticorax nycticorax*) were the most important predators (Blaker, 1969; Siegfried, 1972a). Blaker (1969) indicated that single chicks, which are guarded longer than twins, are too large to be eaten by Night Herons when parental guarding ceases.

Coincident with the start of the Cattle Egret's second week and the onset of its increasing need for energy, grab-feeding develops and the chicks become strongly competitive. At this time also, the chick's bill begins to darken in color, becoming completely black at 10 to 15 days of age, the peak in the period of increased energy requirement. The begging behavior is now violent (Blaker, 1969) and is characterized by the young reaching as high as possible to grab the parent's bill. Since only one chick at a time receives food, the combined effect of reaching and grabbing accentuates the size and age difference between siblings, with the oldest and biggest chick obtaining the most food. After the peak period of energy requirement has passed — at about the end of two and one-half weeks — competition between siblings seems to decrease somewhat. I still lack quantitative data on this phase. However, the black bill begins to pale when the chicks are about four weeks old even though the chicks will be entirely dependent on their parents for food for another two weeks. Blaker (1969) concluded that the function of the black bill in the chick is to prevent the siblings from wasting energy and perhaps inflicting damage by attempting to eat each other. He proved that the yellow bill is a very strong releaser of chick feeding behavior.

Blaker's data (1969) show that when the chick, or chicks, are still being brooded, each parent makes only one collecting trip for food per day. In

## TABLE 1

Mean Weights of Cattle Egret Chicks Early and Late in the Breeding Season*

| *Age of chick in days* | *Chicks hatched in first week of October* | | *Chicks hatched in last week of November* | |
|---|---|---|---|---|
| | *Weight in grams* | *Number of chicks weighed* | *Weight in grams* | *Number of chicks weighed* |
| 2 | 29<br>(22–44) | 11 | 28<br>(25–36) | 6 |
| 3 | 46<br>(31–72) | 10 | 36<br>(29–44) | 5 |
| 4 | 66<br>(40–140) | 9 | 45<br>(29–69) | 6 |
| 5 | 79<br>(45–118) | 10 | 56<br>(32–66) | 5 |
| 6 | 90<br>(87–93) | 3 | 81<br>(71–105) | 4 |
| 7 | 102<br>(70–133) | 11 | 79 | 1 |
| 8 | 105<br>(93–122) | 6 | 105<br>(80–126) | 4 |
| 9 | 123<br>(90–139) | 11 | 129<br>(112–168) | 5 |
| 10 | 160<br>(120–214) | 12 | 148<br>(105–195) | 5 |
| 11 | 152<br>(116–185) | 3 | 136 | 1 |
| 12 | 208<br>(168–256) | 8 | 178<br>(118–219) | 4 |
| 13 | 200<br>(170–214) | 5 | 190<br>(180–200) | 2 |
| 14 | 220<br>(216–243) | 6 | 189<br>(145–230) | 5 |
| 15 | 216<br>(203–237) | 4 | 172 | 1 |
| 16 | 225<br>(207–254) | 6 | 220<br>(210–230) | 2 |

*Weights represent first-hatched chicks of two-chick broods.

chicks older than 10 days in single-chick broods each parent brings food on an average of about once a day; in twins, each parent brings food 1.3 to 1.5 times a day. In the case of single-chick broods, this means that during the time of peak food requirement each parent has to bring in about 50 gm of insect food per visit. Fifty grams of insect food apparently approaches the maximum that a Cattle Egret normally gathers and carries at one time (Siegfried, in prep.). In the light of this, it is hard to see why the frequency of feeding for twins is less than double that for singletons unless parents of twins are approaching the limit of their food-finding capacity. I believe it highly unlikely that the relatively big difference in feeding frequency between single and

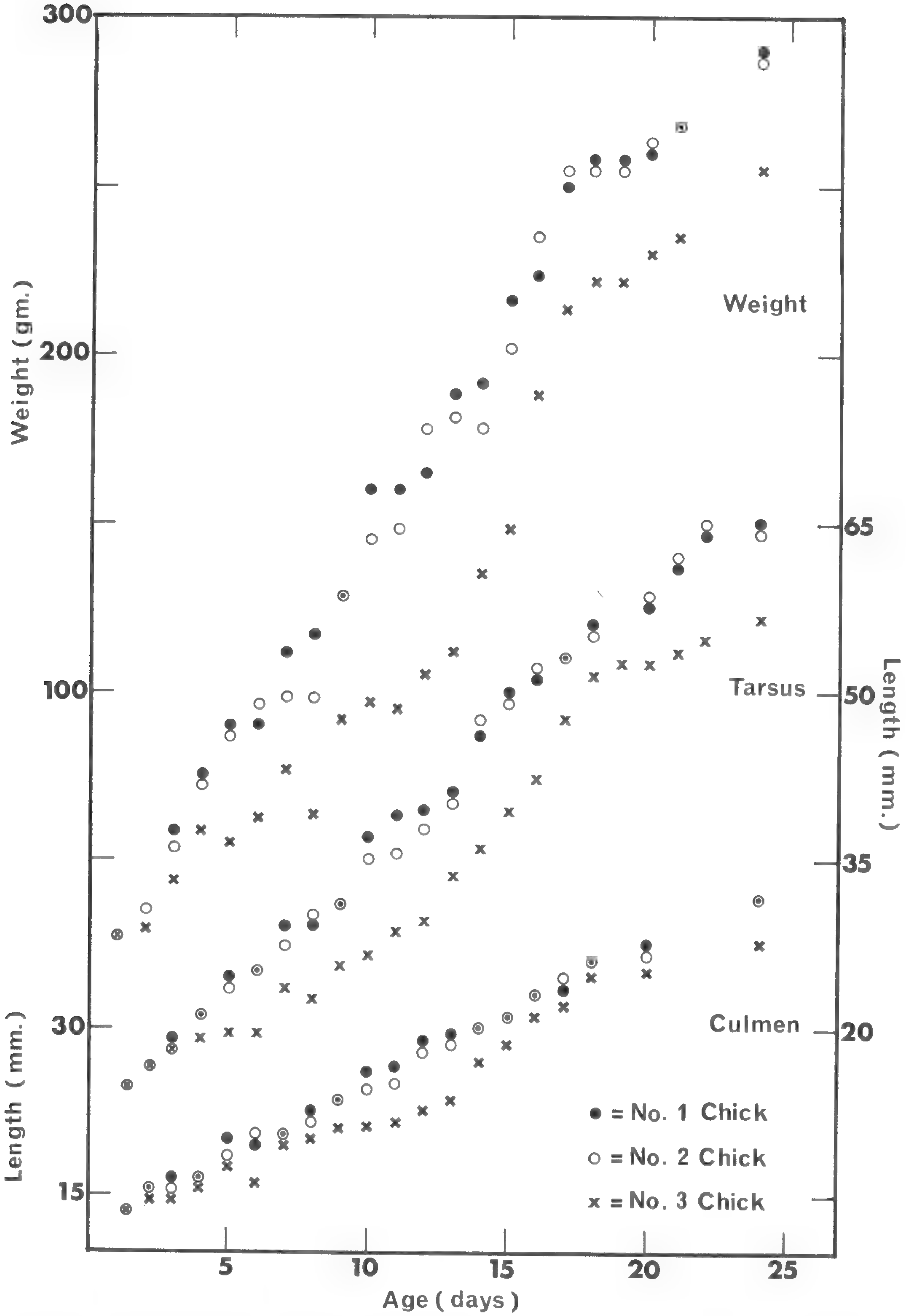

Figure 5. Mean growth curves of body weight, tarsus, and culmen for individual Cattle Egret chicks in a brood of triplets. Data from 15 different broods.

two-chick broods after 10 days of age is entirely due to reduced heat-loss in twins (Royama, 1966). Unfortunately, we have no data on the frequency of feeding for triplets, but my general impression is that their parents never stood idly by as the parents of singletons sometimes did.

## *Discussion*

During its second week of life, a Cattle Egret chick requires daily, on the average, an estimated quantity of energy equivalent to that contained in 95 gm of fresh insect food. At 95 gm per chick, therefore, the parents of a brood of three need to deliver 285 gm of fresh insect food every day. The parent itself requires 122 kcal, 74 gm, of insect food (Siegfried, 1969). Assuming that the parents share equally in the task of feeding the young, we can conservatively estimate that each parent must collect daily 216 gm of insect food for itself and its three chicks, aged about 10 days.

If the parent is capturing grasshoppers, the usual food brought to medium-sized chicks (Siegfried, 1971a, 1972b), and if the average grasshopper 2.0 centimeters in length weighs 0.125 gm, then each parent must capture for its young and for itself 1,728 grasshoppers in a 12-hour day, or one grasshopper every 25 seconds. Although I have no data on the density of grasshoppers on the feeding grounds of the Cattle Egrets in my study area, the rate at which the birds must capture food is a formidable task by any standard. The crucial question is whether the needs of three chicks exceed the food-gathering capacity of the parents. It seems that this is the case, and may be the normal situation in this area.

Of course, in practice, grasshoppers are not the only food of the Cattle Egret nestlings, and, as shown elsewhere (Siegfried, 1971a; 1972a), the proportion of vertebrates such as frogs increases in their diet as they grow older. Similarly, and at the same time, there is a gradual increase in the size of the food items taken by the young as they themselves increase in size. To what extent, if any, the parents may be actually selective in capturing food for young of different ages is not known. Nevertheless, in the study area, relatively small insects, particularly grasshoppers, do make up the bulk of the diet in two-week-old chicks. For this reason I have included estimates of the parent-chick energy budget in terms of insect food. I suggest that the Cattle Egrets in my study area seldom rear more than two chicks at a time primarily because they have to rely mainly upon small insects for food.

The second point to consider is the low rate of food delivery. When food is scarce, a parent can theoretically increase the rate of delivery by increasing its own effort. However, there is a practical limit to which a parent can expend effort without endangering its own survival. For every food-resource level there must be an optimum effort, and different levels will influence the rate at which the parent delivers food to the young. One and a half feedings a day by each parent is considered close to the optimum level on which Cattle Egrets can operate in the study area. If the parents of two-week-old triplets have to deliver about 300 gm of insect food daily, it means at least three feedings of 50 gm each by each parent per day. Since this is double the feeding rate recorded for twins, it is not surprising that so few triplets survive intact.

Lack (1954) advanced the thesis that hatching at different times is an adaptation which permits an adjustment in the size of the brood in response to unpredictable fluctuations in the availability of food. This mechanism allows the greatest possible number of young to be raised at various levels of food availability. There can be little argument against the view that this mechanism operates in Cattle Egrets. In fact, the overt aggression of chicks toward their siblings at feeding times, the violent and exaggerated begging, and the actual methods of feeding (Blaker, 1969) all point toward behavioral strategies evolved in response to competition for food. The very conspicuous form of feeding and begging behavior could presumably only have evolved in a species relatively free from predation. On the other hand, we might argue that if the amount of food that a parent can supply at one time limits the number of surviving young in a brood, selection, in the absence of predators, could have favored the evolution of a slower rate of growth — if it were advantageous.

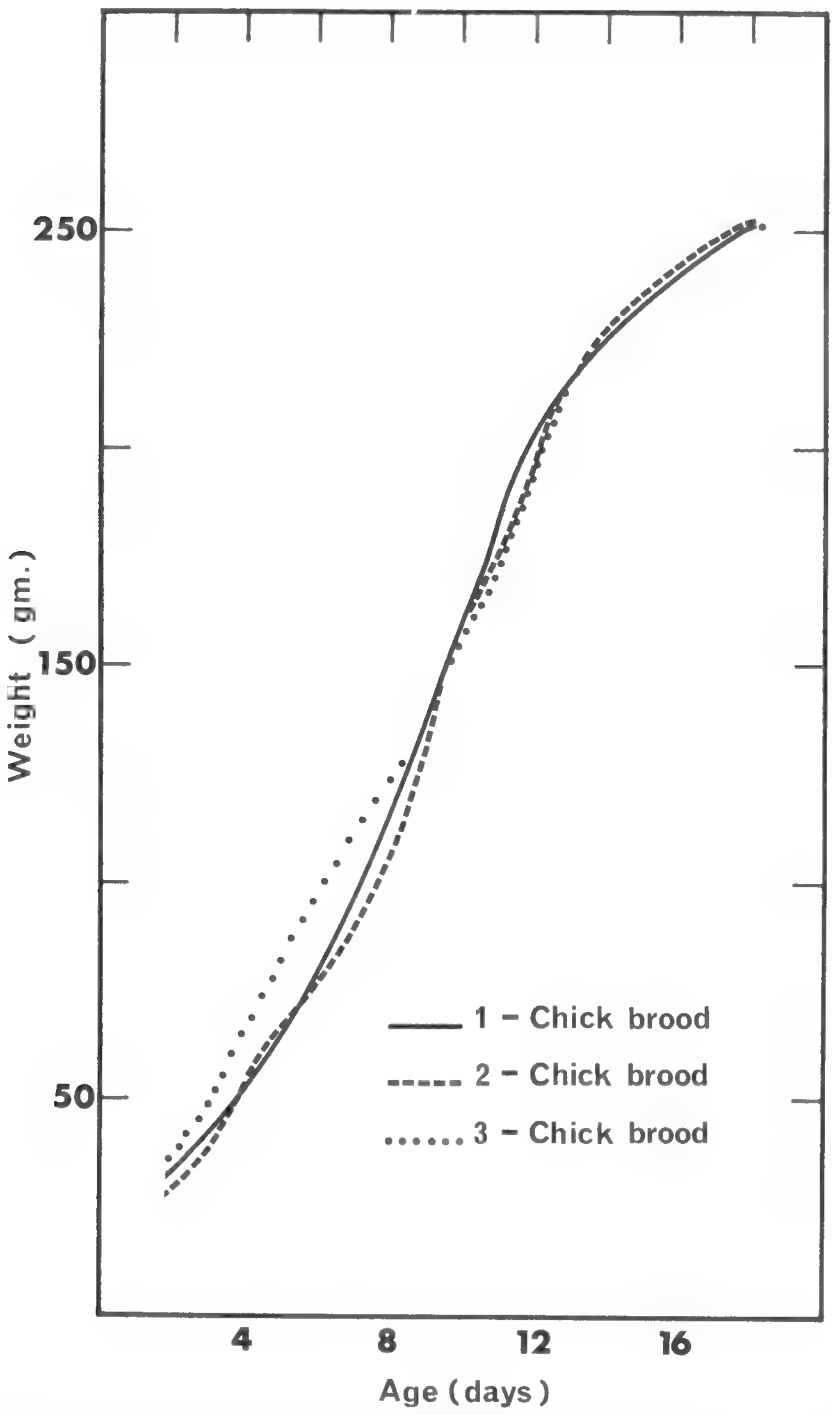

Figure 6. Average growth in body weight for individual first-hatched Cattle Egret chicks in broods of one, two, and three. Data from 37 chicks. Curves smoothed.

This does not, however, explain fully the consistent difference between the average clutch size and the average brood size at fledging — normally three eggs are laid and hatch, but seldom do the parents succeed in raising more than two chicks at a time (Siegfried, 1972a). Or to phrase it another way, why should the average clutch size not correspond more closely to the average number of young reared per brood? Preliminary observations indicate that environmental conditions in the study area during the breeding season are not so unpredictable and variable from year to year that they could favor a mechanism which would permit a disproportionately large average clutch size to correspond to ultra-favorable environmental conditions, which might occur often enough to yield significantly increased productivity. In short, there seems to be no advantage attached to southwestern Cape Cattle Egrets maintaining a clutch size above the normal optimum needed to correspond to the relatively stable and predictable food resources available for feeding the young.

In my view, the most probable answer is that the present normal clutch of Cattle Egrets in the southwestern Cape evolved under conditions in the immediate past, different but not necessarily less predictable and less stable than those in the study area. Another important qualification is that these areas where the birds evolved were, and still are, undisturbed and natural with a suspected higher ecological availability of food during the breeding season.

Before commenting further on this point, we should remember that the Cattle Egret's history of breeding in extensively man-modified habitat, especially in the temperate regions of South Africa, goes back no more than about 50 years — 30 years in the study area. Second, extensive, long-distance immigration and emigration over much of Africa south of the Sahara ensures a continuing exchange of genes within the subcontinental populations (Siegfried, 1970).

Returning to the ecological availability of food, I suggest that the yield of food per unit effort might be greater in natural areas than in certain man-modified habitats, such as the Cape area. Possibly the levels of availability of relatively large prey, such as frogs, are generally more favorable in the undisturbed areas — the large marshes, for example, where some Cattle Egrets breed. Although a man-modified habitat might support a greater total biomass of prey — presumably mainly insects in the study area — it is conceivable that the proportionately higher levels of larger prey in the natural areas might yield a more efficient return for equal effort.

In this context, an increased return in food capture would permit a feeding rate to cope with the demands of a three-chick brood at its peak of energy requirement. To give a hypothetical example: assuming that frogs have about the same water content and caloric value as lean beef, then a delivery rate of two 25 gm frogs, three times per day, by each parent would satisfy the maximum daily demand of a three-chick brood. Developed agricultural land may yield food at a year-round rate quite adequate for non-breeding birds, but may not fulfill the birds' extra demands for successful breeding.

Further indirect evidence that large, single food items, and not small insects, were, and presumably still are, the most important constituents in the diet of half-grown nestlings is perhaps provided by the size of the chick's gape (see Skead, 1966); the extensive distention of the mandible facilitates the successful passing, from parent to chick, of large items, such as frogs. It is further possible that the peck-feeding period, which precedes the grab-feeding period, permits chicks to select the right size food items from the apparently non-selective bits brought in by the parents. In effect, this would prevent chicks from trying to swallow items so large that they might choke.

We need detailed studies of the ecology of the Cattle Egret in the area of its original range and the areas of its recent geographic spread. In particular, we need information about Cattle Egrets breeding in a completely natural, undisturbed "tropical" area in order to evaluate properly some of the findings reported in this paper. In semi-tropical Florida in North America, Jenni (1969) found Cattle Egret nestling mortality to be relatively low; the parent birds appeared able to provide sufficient food for all their young. Apparently, an abundance of food was available. However, Jenni made his observations from 1958 to 1960, only eight years after Cattle Egrets first nested in North America. Possibly the relatively low mortality reflected an unsaturated breeding population exploiting a vacant feeding niche.

## *Summary*

This paper reports the growth and food requirements of nestling Cattle Egrets (*Ardeola ibis*) in a man-modified habitat in the southwestern Cape Province, South Africa, where this species normally fails to raise successfully more than two chicks out of broods of three or four. An examination of the energy budgets of parents and young indicates that the amount of food required to raise more than two chicks normally exceeds the food gathering capacity of the parents. In the study area, breeding Cattle Egrets captured primarily small grasshoppers. This suggests that the yield of food per unit effort expended on gathering it is greater in undisturbed natural areas than in the man-modified southwestern Cape. The undisturbed areas, where a proportionately greater availability of larger prey, such as frogs, is available, probably yield a more efficient return and result in closer agreement between the average number of young hatched and the average number of young fledged per brood.

### *Acknowledgments*

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# THE DISTRIBUTION AND ECOLOGY OF THE PUERTO RICAN WHIP-POOR-WILL, AN ENDANGERED SPECIES

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Photographs by the authors

Caprimulgids are characteristically among the least known of a region's avifauna, but few can match the obscurity of the Puerto Rican Whip-poor-will (*Caprimulgus noctitherus*) over the past century. Prior to 1961, only one specimen was known (Cory, 1889) although subfossil bones had been identified by Wetmore (1919, 1922). Wetmore (1919, 1922, 1927) saw what he thought was this species in 1911, the last view of the bird for 50 years. During this period various authors considered the Puerto Rican Whip-poor-will extinct (Bond, 1956, 1961; Greenway, 1958; McCandless, 1958; Peters, 1940), assuming that the mongoose (*Herpestes javanicus*), introduced in 1877 (Wadsworth, 1949; Wolcott, 1953), had decimated the species.

In 1961, Reynard (1962) rediscovered the species in the xeric, or dry scrub, at Guanica in southwestern Puerto Rico. He collected one male and heard "six or more" birds singing nearby. Surprisingly, very little work resulted from this discovery, and the status of the species remained obscure. Leopold (1963) estimated the Guanica population as "some 25 pairs, confined to the Guanica Forest," and speculated that populations might be found on the limestone hills near Ponce; Bond (1962) reported that "numerous individuals were heard on the semi-arid hills near the coast," indicating a "sizeable extant population." He presumably based his statement on Reynard's observations. Biaggi (1970), however, only concluded that the species may still exist in Puerto Rico.

Following Reynard's work, J. B. McCandless (pers. commun.) organized Puerto Rican Whip-poor-will censuses in Guanica and estimated that as many as 100 birds remained within the forest. Because it had existed undetected for so long, the population was considered very rare and very local, and both the 1968 Committee on Rare and Endangered Wildlife of the United States Department of Interior and the International Union for the Conservation of Nature and Natural Resources placed *C. noctitherus* on their lists of rare and endangered birds (Vincent, 1966).

## Taxonomic Opinions

Opinions vary as to the taxonomy of this species. It is closely related to and derived from the Whip-poor-will (*Caprimulgus vociferus*) of North America, a common and widespread bird. Bond (1945), following Peters (1940), has consistently regarded the bird as an insular race of the continental species, *C. vociferus noctitherus,* a decision adopted by Greenway (1958). Wetmore was convinced in 1919 that the smaller and differently colored Puerto Rican bird was specifically distinct, a position he maintained through the years (Wetmore, 1919, 1922, 1927), and one that the Committee on Rare and Endangered Wildlife (1968), Vincent (1966), and Mayr and Short (1970) have followed. The vocalizations, described by Reynard, are completely different in structure from those of *C. vociferus.* Since song appears to be an important element in the courtship of caprimulgids and may serve to maintain reproductive isolation between closely related species, we follow the taxonomic decision of Wetmore and regard the Puerto Rican birds as an endemic species, *C. noctitherus,* at the same time recognizing the difficulty of properly allocating closely related populations isolated on islands. In this paper, for the sake of brevity, we frequently refer to the Puerto Rican Whip-poor-will as simply *noctitherus* or the Whip-poor-will.

### *Methods*

In 1968 we began a series of studies of the Puerto Rican avifauna. From 23 January 1969 to 8 October 1971 we made 15 trips to Guanica Forest and the surrounding areas to determine the distribution and ecology of the Puerto Rican Whip-poor-will. We visited southwestern Puerto Rico in every month except April and September. In Guanica Forest, where *noctitherus* was known to occur, we established linear census routes along jeep trails and abandoned roads in order to determine population density and distribution within the reserve. We marked each route every 100 meters over a minimum distance of one kilometer and conducted all censuses before dawn during periods of peak calling. In 30 minutes, we walked 1.0 to 1.6 km, stopping every 100 meters to record the approximate distance and direction of each Puerto Rican Whip-poor-will heard; we tabulated individuals, recorded in the previous 100 meters, separately and did not record birds calling ahead until they were within the section being censused.

In addition, we searched for *noctitherus* in likely habitats throughout Puerto Rico and on all major offshore islands (Table 1 and Figure 1). Because members of this family can be difficult to find, we camped overnight in as many areas as possible. We discovered additional populations in Susua Commonwealth Forest and the Guayanilla hills, and established four census routes in the Susua Forest.

Because our time was limited, we made no attempt to study the breeding biology in detail, but we discovered and examined two nests, and the data from these, together with annual fluctuations in calling, provide a picture of the breeding biology. At the same time, we made incidental observations on the West Indian Nighthawk (*Chordeiles gundlachii*) and compared its ecology with that of *noctitherus.*

## Past Distribution

Our knowledge of the former distribution of *noctitherus* rests on three fragments of information (Figure 1): One skin, taken by Streator in Bayamon in 1888 (Cory, 1889), bones in natural cave deposits from Morovis (Wetmore, 1919, 1922), and Wetmore's single sight record from Rio Piedras. The Morovis deposits consisted of five humeri and one metacarpal, found in deposits of bat guano and animal remains in two separate cave systems and estimated to be less than 2,000 years old. These remains, not associated with human activity, may have been carried into the cave by owls (Wetmore, 1922).

Bayamon, Morovis, and Rio Piedras lie north of the Cordillera Central, Puerto Rico's backbone mountain range, and Morovis and Bayamon lie within a large expanse of limestone topography, called karst, that extends from Bayamon to the west coast, covering most of the northwestern third of the island (Figure 2). This region was originally covered with a "moist limestone forest" described along with other forest types by Little and Wadsworth (1964). Rio Piedras borders this limestone region to the east; its original flora was similar to that in the limestone and is known as the "moist coastal forest." As the caves near Morovis lie within the karst region, and limestone "magotes," or domes, surround Bayamon, it is likely that the original range of the Puerto Rican Whip-poor-will was coextensive with that of the moist limestone forest, and included at least part of the moist coastal forest farther east that extended south on both the western and eastern coasts (Figure 2). It is possible that the Whip-poor-will ranged south as well.

All records from the south coast are recent; Reynard discovered the first birds there in 1961. He noted, however, that residents in the region have heard the bird at least since 1900 (Reynard, 1962). At present, we know of three populations in the arid southwest coast. Two of these, at Guanica and the hills above Guayanilla, occur on limestone soils (Figures 1 and 2) in "dry limestone forest." Using the present distribution as a guide, it is likely that the Puerto Rican Whip-poor-will originally inhabited the limestone forests of the south coast. The third population is located in secondary scrub vegetation in Susua Commonwealth Forest, a region that is now similar to Guanica in flora and structure, but in the past, when it was a virgin "lower cordillera forest," was much lusher. In the Susua Forest, *noctitherus* is presently limited to the drier, more open sections of the reserve and has not been found in the riparian forests or the denser scrub at elevations above 350 km. It is possible that the species originally inhabited some of the cordilleran forests at lower elevations. In view of the whip-poor-will's present distribution on the south coast, it is also reasonable to assume that its range once extended beyond the dry limestone into the dry coastal forest, possibly encircling the island.

The present distribution of insectivorous birds and the variation in the density of insects in habitats of different elevation in Puerto Rico also provide an insight into the former range in the montane rain forests of the upper slopes. The higher elevations in the Sierra de Luquillo and the Cordillera Central receive more than 2,000 millimeters of rainfall per year, more than three times that received on the south coast. In Luquillo Forest, the wettest part of the island with 5,000 mm of rain per year, birds that capture their insect prey on the wing are notably absent (Kepler and Kepler, 1970), whereas they are common and conspicuous in the southwest. Studies of insect abundance, measured by sticky fly-paper traps set out in both Luquillo and Guanica, show that flying insects are less common the year around at higher elevations (Kepler and Kepler, in prep.), and insect abundance can be expected to be similarly depressed in the Cordillera Central. We infer, therefore, that the upper slopes would not have provided enough food for *noctitherus* and that the species did not occur high in the mountains. Thus, the original range probably covered most of the coastal plain on both sides of the island, possibly connecting on the east and west coasts, and extended a short distance up the slopes of the mountains.

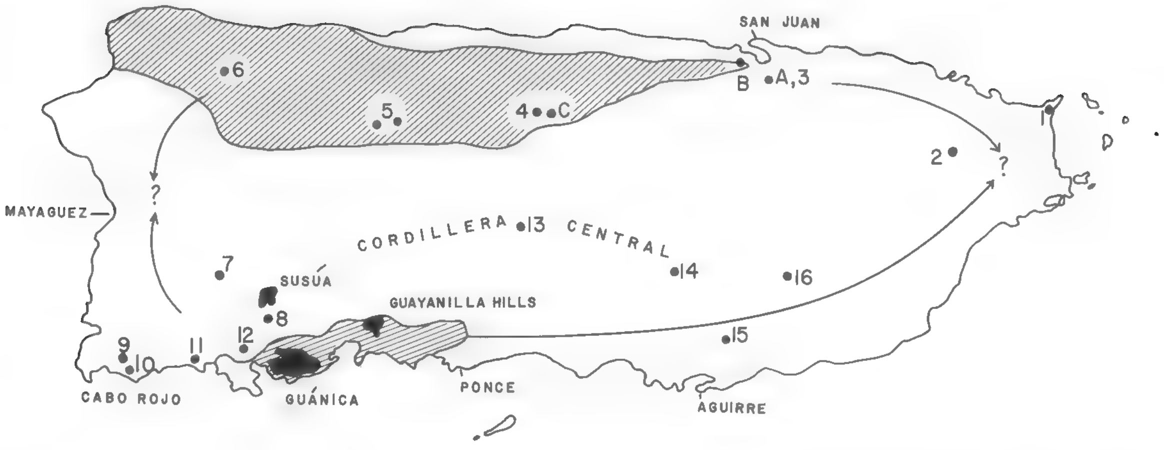


Figure 1. Map of Puerto Rico. A, B, and C mark the locations of previous Whip-poor-will records; diagonal lines indicate its possible former range; solid area shows its present known distribution. Numbers show areas searched unsuccessfully and correspond to names listed in Table 1.

## *Present Distribution*

The Puerto Rican Whip-poor-will appears to be restricted to three areas on the southwest coast (Figure 1), although McCandless (pers. commun.) recorded a single bird, probably a stray, giving full song near Mayaguez. We found no evidence of birds outside the plotted range, although we spent 32 nights searching throughout Puerto Rico and its offshore islands (Table 1). In many cases we searched hills near Guanica without success while Whip-poor-wills continued calling within this Reserve. Both Rio Abajo and Guajataca Forests are within the historic range and have very low human densities in or around them. There are thousands of limestone domes within the karst country that offer conditions similar to those found in the southwest, including a representative xeric avifauna, but we did not find Whip-poor-wills there, presumably because the limestone valleys often hold water, and rainfall within the region is high enough and frequent enough to provide a constant water supply for mongooses. Although there are no records for *noctitherus* from any of the offshore islands, most of which are xeric and mongoose-free, we listened, without success, on all the major Puerto Rican islands in the hope that we could locate an isolated population.

Two other areas in Puerto Rico might still harbor small populations — the lower slopes of the Cordillera Central in Maricao Commonwealth Forest, which is very similar to Susua, and the limestone hills east of Ponce. We doubt that there are any populations outside these areas. Thus, we believe that the Whip-poor-will inhabits 3,200 hectares, approximately three per cent of its probable former range — the limestone regions — and only 0.7 per cent of the total land surface of the island.

### Guanica Commonwealth Forest

*General Description of Forest.* — Guanica Forest, protected since 1919, consists of an 850-hectare unit of low profile, west of Guanica Bay, and a larger, 2,800-hectare unit to the east. The western unit does not have Whip-poor-wills; in all the following discussions "Guanica" refers to the eastern part of the forest reserve.

TABLE 1

Areas Searched for Puerto Rican Whip-poor-will

1969–1971*

| *Area number* | *Location* | *Dates* | *Number of visits* | *Time of day* | *Forest type* |
|---|---|---|---|---|---|
| | Puerto Rico | | | | |
| 1** | Cabeza Chiquita | 22–23 February 1970 | 1 | overnight | moist coastal |
| 2 | Sierra de Luquillo | 1968–1971 | 3 years | overnight | luquillo |
| 3 | Rio Piedras | 17 November 1968 | 1 | dusk | moist coastal |
| 4 | Rio Cialitos | 22 October 1971 | 1 | dawn | moist limestone |
| 5 | Rio Abajo Forest | 14–15 November 1969 | 1 | overnight | moist limestone |
| 6 | Guajataca Forest | 28–30 July 1970 | 2 | overnight | moist limestone |
| 7 | Maricao Forest | 10–11 July 1971 | 1 | overnight | lower cordillera |
| 8 | Cerro la Torre | 19 February 1970 | 1 | dusk | lower cordillera |
| 9 | Sierra Bermeja — Nth | 11 November 1969 | 1 | dusk | dry coastal |
| 10 | Sierra Bermeja — Sth | 25 May 1970 | 1 | dusk | dry coastal |
| 11 | Parguera Hills | 23 May 1970 | 1 | midnight | dry coastal |
| 12 | Cerro de Abra, El Peñon | 12 December 1970 | 1 | dusk | dry limestone |
| 13 | Toro Negro Forest | 7–9 December 1970 | 3 | overnight | upper cordillera |
| 14 | Aibonito | 1969–1970 | 10† | overnight | upper cordillera |
| 15 | Carmen-Guayama | 22 April 1970 | 1 | dusk | lower cordillera |
| 16 | Carite-Guavate Forest | 22–23 April 1970 | 1 | overnight | upper cordillera |
| | Offshore Islands | | | | |
| | Mona | 6–9 June 1969 | 3 | overnight | dry limestone |
| | Monito | 5–6 June 1969 | 1 | overnight | dry limestone |
| | Desecheo | 29–30 June 1970 | 1 | overnight | moist coastal |
| | Culebra Islands: | | | | |
| | "mainland" | October 1968;<br>4–6 January 1971 | 4 | overnight | moist coastal |
| | Cayo de Luis Peña | 13–14 May 1971 | 1 | overnight | moist coastal |
| | Cayo Lobo | 19 June 1971 | 1 | overnight | moist coastal |
| | Culebrita | 10–11 June 1971 | 1 | overnight | moist coastal |
| | Cayo Norte | 15–16 April 1971 | 1 | overnight | moist coastal |
| | Vieques | 20–21 July 1971 | 1 | overnight | dry limestone |
| | Vieques | 21–22 July 1971 | 1 | overnight | moist coastal |

*Table excludes three areas where *C. noctitherus* occurred: Guanica Commonwealth Forest, Susua Commonwealth Forest, and Guayanilla Hills.

**Numbers for locations correspond with numbers shown on map, Figure 1.

†Area censused 10 times over a one-year period by Mr. and Mrs. Del Buerge, residents in rural Aibonito.

The forest, while not virgin, is the best example of dry limestone forest remaining on the island (Figures 3 and 4). The annual rainfall is 750 mm, contrasting with an annual water loss through evaporation and plant transpiration of 2,000 mm. The entire forest grows upon porous Tertiary limestone soils. As a result, there is no standing or running fresh water anywhere within its boundary. The elevation ranges from sea level to 230 meters. The semi-deciduous vegetation consists of hardwood trees on the tops of the limestone hills, normally above the 75-meter contour, and below this, particularly on the southern seaward slopes, a cactus forest, composed primarily of *Cephalocereus royenii* and *Opuntia rubescens* mixed with the species of trees found

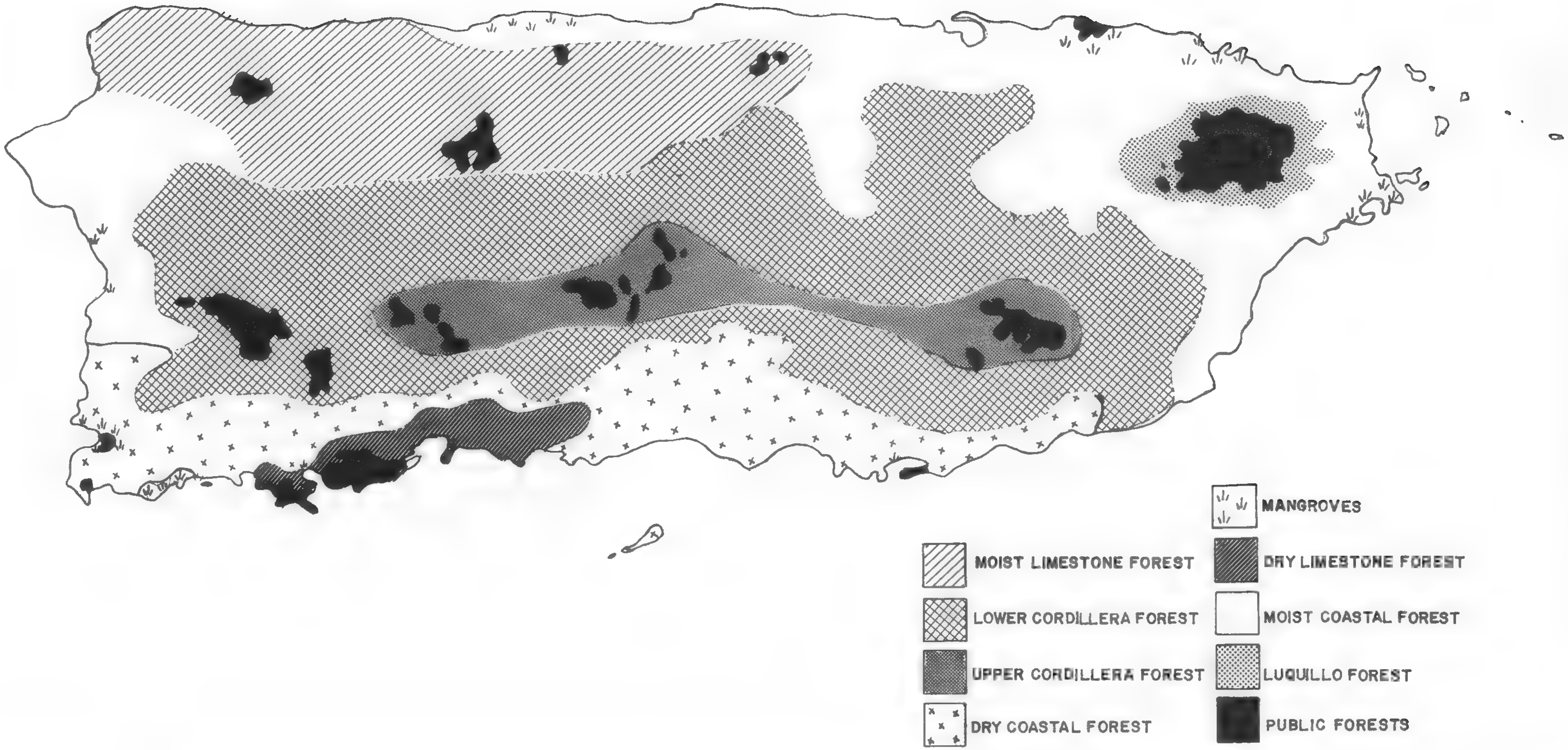

MANGROVES
MOIST LIMESTONE FOREST
DRY LIMESTONE FOREST
LOWER CORDILLERA FOREST
MOIST COASTAL FOREST
UPPER CORDILLERA FOREST
LUQUILLO FOREST
DRY COASTAL FOREST
PUBLIC FORESTS

Figure 2. Vegetation map of Puerto Rico, showing major forest types and Commonwealth and Federal forest reserves (after Little and Wadsworth, 1964).

higher. The canopy is four to five meters high, with some trees reaching six to seven meters. Important species include *Pisonia albida* (Nyctaginaceae), *Swietenia mahogoni* (Meliaceae) planted in some valleys, *Acacia farnesiana* (Leguminoseae), and *Bursera simaruba* (Burseraceae). Little and Wadsworth (1964) listed the important trees. There is neither a well-marked stratification nor a well-developed epiphytic flora, but the ball or bird's-nest bromeliad (*Tillandsia recurvata*) is abundant. Although dry, the region is not a desert, as stated by MacArthur and Wilson (1967), and Guanica supports a greater species diversity of trees (Roy Woodbury, pers. commun.) and land birds (Kepler and Kepler, 1970) than any other part of the island.

Since Guanica harbored the only known population of *noctitherus,* we began our work there. And we continued to concentrate our efforts there even after we had discovered the two additional populations, each less than 10 km away, because of the greater density of birds, the superior system of trails, and the lack of disturbance. All our census routes are shown in Figure 5 and listed in Table 2; the major routes were the West, East, North, and Tamarindo. We censused other locations primarily to determine the limits of the population within Guanica and to detect any variations in density.

*Distribution of Whip-poor-will.* — *C. noctitherus* is not uniformly distributed in Guanica Forest (Figure 5). The population is centered on the higher slopes of the central hills (Figures 3 and 6), broadly coincident with the semi-deciduous forests, and is largely absent from the south-facing slopes below 75 meters, which are dominated by cactus, open patches of grassland and scrub, and thickets of *Agave.* The transition between the two habitats is, in many locations, strikingly abrupt. Four of our census routes passed this boundary, and in three of them *noctitherus* was restricted to the higher forest. Standing in the transition, we could regularly listen to several birds calling loudly above and, at the same time, hear no sound from the slopes below. On Gate Trail — the only one where the land rose gradually with no obvious transition point — the only three Whip-poor-wills recorded were above 75 meters. We have divided the Tamarindo Trail, the only major census route that crossed from the hills to the flats below, into "upper" and "lower" sections — above and below 75 meters. Only seven of the 23 *noctitherus* recorded along the Tamarindo were below 75 meters. We found four of these on two limestone ridges, 25 meters high, that separated flatter stretches above and below. The vegetation at this point resembled more closely that found at higher elevations. We heard two of the remaining three birds only in February, when calling was at peak levels throughout Guanica, suggesting that territorial encounters are frequent and vigorous at this time, with the possible emigation of young or subordinate birds from the central population. We never heard these two later.

In Jamaica, the presence of abundant *Cereus* cactus in the dry limestone forest indicates human disturbance; undoubtedly, this is true in Puerto Rico as well. The presence of *Agave* and grassy meadows and the weedy appearance of many lowland areas (Figure 7) contrast sharply with the forests higher up (Figure 3). In similarly disturbed areas above 75 meters, *noctitherus* is absent. A measure of the presence or absence of some birds that thrive in man-made clearings and second-growth vegetation can also determine the amount of disturbance. We compared the census results for the Mockingbird (*Mimus polyglottos*) with those of *noctitherus* on lower Tamarindo Trail and West Road (Table 3). The Mockingbird rarely occurs in virgin forest or dense

### TABLE 2

### Summary of Whip-poor-will Censuses, Guanica Forest

| *Census route** | *Census date(s)* | *Number of counts* | *Number of Whip-poor-wills* | *Number per kilometer* | *Distance censused in kilometers* | *Highest count per kilometer* |
|---|---|---|---|---|---|---|
| 1. North Road | all year | 6 | 54 | 8.3 | 6.5 | 13.0 |
| 2. East Road | all year | 8 | 111 | 8.4 | 13.2 | 11.9 |
| 3. West Road | all year | 9 | 98 | 9.2 | 10.6 | 13.1 |
| 4a. Upper Tamarindo | all year | 6 | 16 | 5.3 | 3.0 | 5.7 |
| 4b. Lower Tamarindo | all year | 6 | 7 | 1.7 | 4.1 | 6.6 |
| 5. Main Road | 12 November 1969 | 1 | 12 | 12.0 | 1.0 | |
| 6. Ballena Road | 13 July 1969 | 1 | 6 | 4.6 | 1.3 | |
| 7. Dynamite Road | 11 July 1969 | 1 | 7 | 7.0 | 1.0 | |
| 8. Gate Road | 13 July 1969 | 1 | 3 | 1.9 | 1.6 | |
| 9. Barrio Susua Baja | 14 March 1969 | 1 | 10 | 10.0 | 1.0 | |
| 10. Susua Baja Trail | July 1970; May 1971 | 2 | 23 | 7.2 | 3.2 | |
| 11. Guanica Bay | 14 March 1969 | 1 | 6 | 3.3 | 1.8 | |
| 12. Beach Road | 13 July 1969 | 1 | 0 | 0.0 | 1.5 | |
| Total | | 44 | 353 | | 49.8 | |
| Average | | | | 7.1 | | |

*Numbers of census routes correspond to those shown in Figure 5.

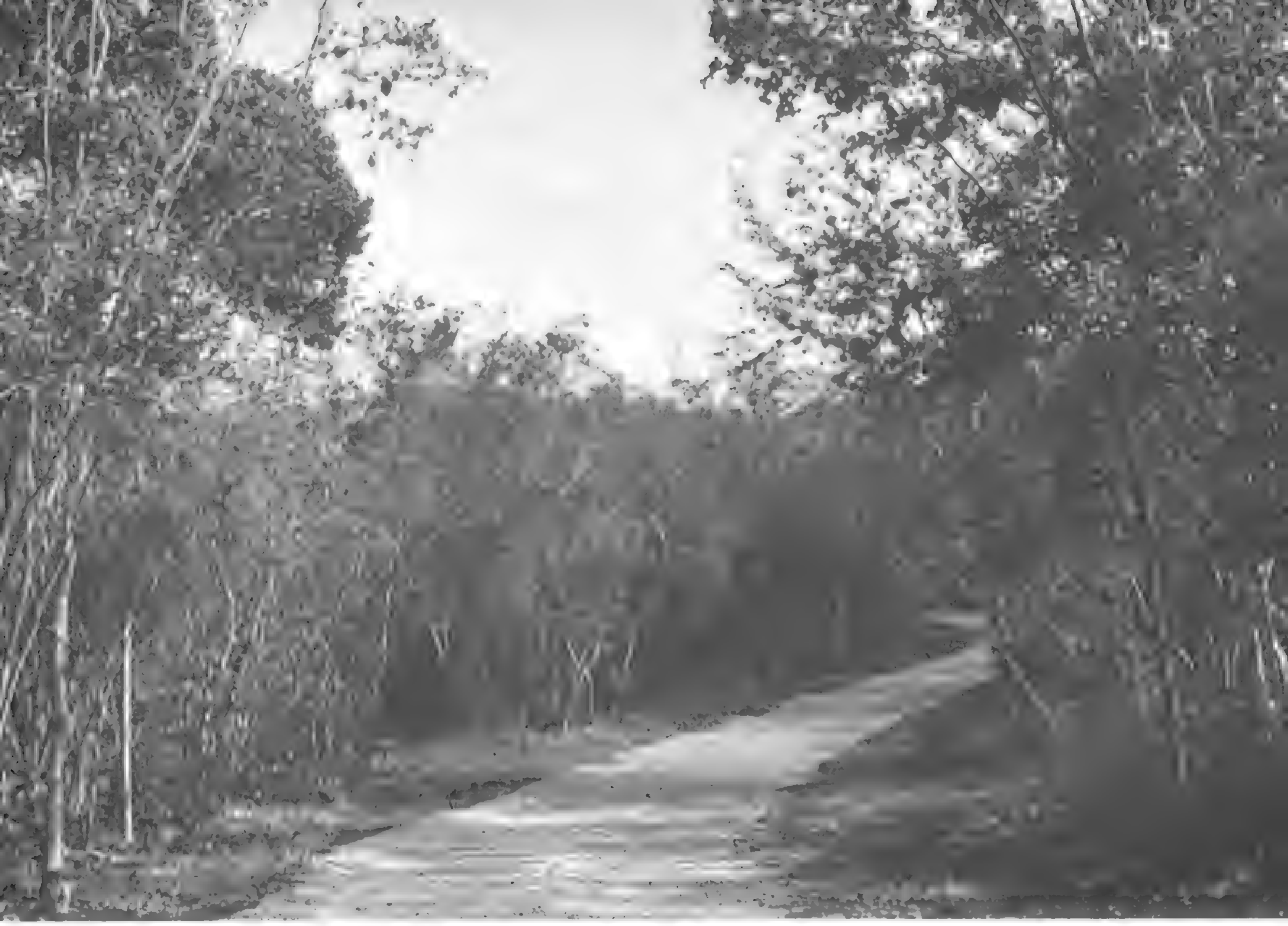
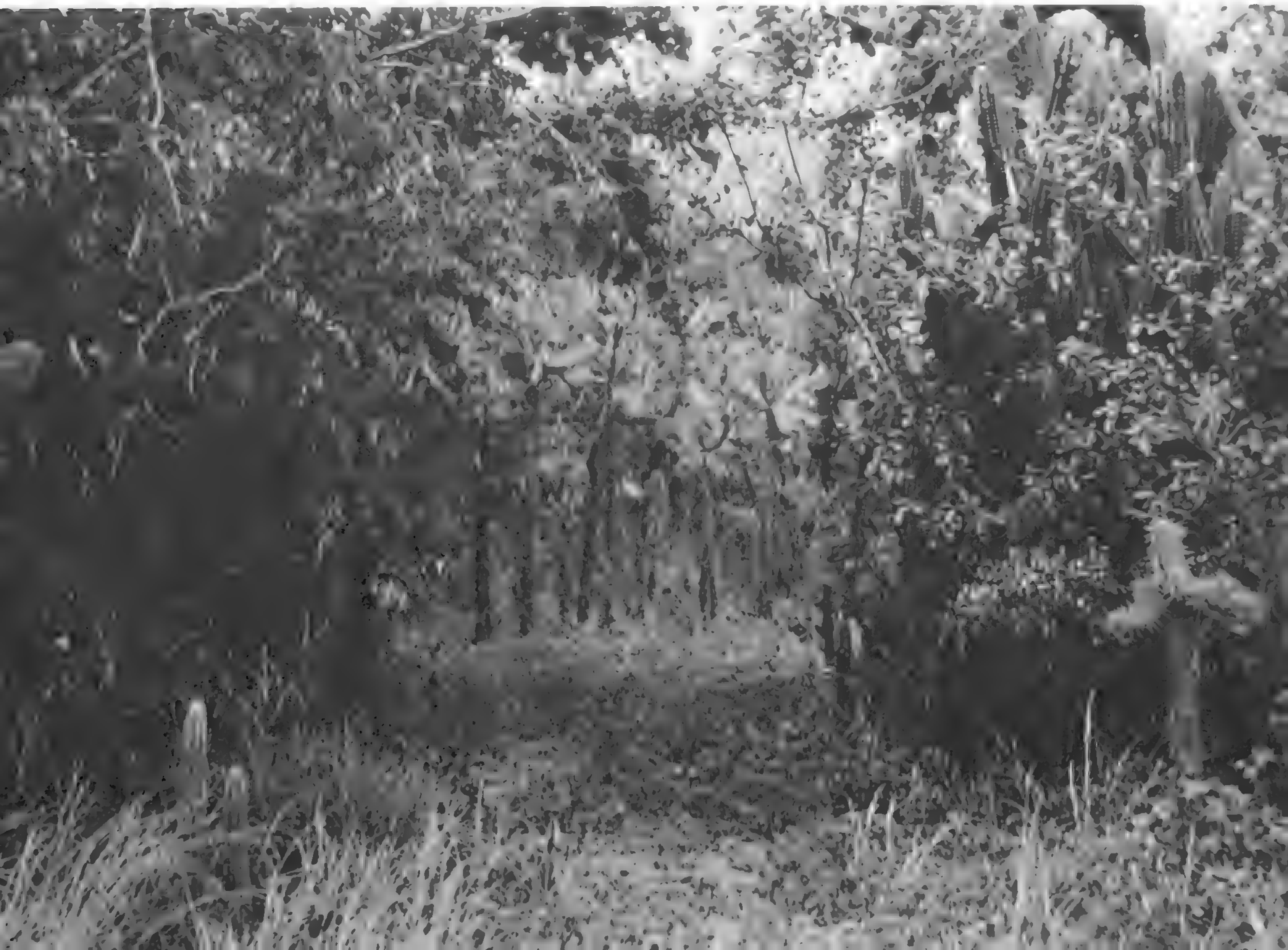


Figure 3 *(above)*. Dry limestone forest in the center of the range of the Puerto Rican Whip-poor-will, Guanica Commonwealth Forest, Puerto Rico.

Figure 4 *(below)*. Cactus forest on the ocean-facing southern slopes below 75 meters, Guanica Commonwealth Forest, where Puerto Rican Whip-poor-wills are uncommon.



woodland anywhere in Puerto Rico, and in Guanica is abundant in those parts of the forest in which *noctitherus* is rare ($X^2 = 27.61$, $P < 0.001$). The areas, used by *noctitherus* in general, lack grass or brush at ground level. The vegetation is fairly open, rather intermediate between the dense tangles and open meadows that alternate in the disturbed areas. We made no quantitative study of these differences, but believe that the Whip-poor-wills respond primarily to the density of the vegetation and the openness near the ground; forest such as that shown in Figure 3 appears to be optimal.

*Population Density.* — From linear census figures one can estimate population density if he knows the range at which he can detect the birds and the percentage of birds perceived at various distances (Emlen, 1971). By walking away from calling *noctitherus* we determined that we could hear them normally from 300 meters, but only rarely at greater distances. Since we can hear almost all birds calling at this distance, and we almost never see them, we do not need to correct for detectability under various conditions, as discussed by Emlen. We have, therefore, converted our linear census results directly into density figures by assuming that each one-kilometer census covers a 600-meter swath, or 60 hectares.

Our results range from 1.7 to 13.1 Whip-poor-wills per km, depending on season and location, and from 4.4 to 13.1 for all censuses conducted in prime habitat. The average and maximum numbers of calling birds is remarkably constant for the three main routes. Table 2, Numbers 1–3, suggest that the territorial requirements are similar throughout the central portions of Guanica Forest.

Guanica Bay Trail, Route 11, passed above a fertilizer plant, now closed but active during the study, whose effluents badly damaged the forest above it. We found no Whip-poor-wills in this disturbed section, and the low overall average reflects this. Because Routes 1–3 were in the center of the range and the most regularly covered, we have used censuses from them to estimate territory size and the total Guanica population. Thus, the average number of calling *noctitherus* is 8.7 birds per km, or per 60 hectares, with one pair of birds per 6.9 hectares, or one pair per 17.2 acres. We have also used the average of the three high counts to estimate maximum population size, a better estimate of overall density in that it does not include low counts during nesting and, presumably, includes the largest number of calling males. We found an average high of 12.2 Whip-poor-wills per km, one pair per 4.9 hectares, or 12.1 acres.

The region inhabited within and adjacent to Guanica Forest was plotted from topographic maps using both the 75-meter contour and the vegetation limits to delineate suitable habitat (Figure 5). The resultant area was calculated by laying a 100 by 100-meter grid over the map and counting all the sections it contained; grids bisected by the habitat edge were counted as one hectare only if more than half the grid was within the suitable habitat. The resulting figure of 2,286 hectares was rounded to 2,300 hectares. This takes into account all our knowledge of Guanica, including disturbed areas within the forest above 75 meters that did not contain Whip-poor-wills, and one detached hill to the north of barrio Susua Baja that did (Figure 5).

In estimating the total Guanica population, we used both sets of census figures. Although Tyler (1940) reported a female *Caprimulgus vociferus* once giving song, we assume that only males ordinarily sing and that each calling bird represents a pair. The maximum figures are probably the most accurate

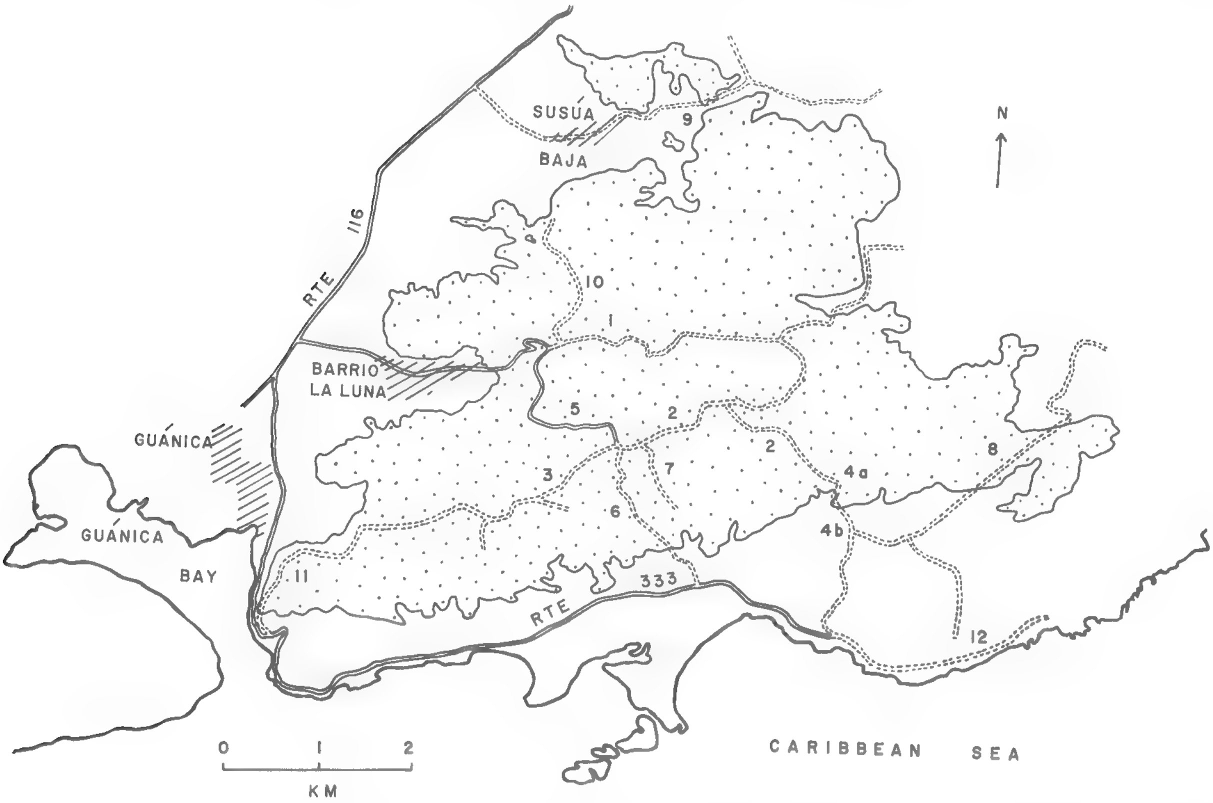


Figure 5. Map of Guanica Forest and adjacent areas. Dark line encloses the vegetated land above 75 meters elevation; stippled area indicates the range of the Whip-poor-will; numbers along the roads refer to census routes in Table 2.

in that a higher percentage of birds present were included in the count. It could err on the high side if nonbreeding males sing without holding breeding territories or are later forced from the best habitats as the Tamarindo sightings suggested. We doubt that we counted females. We never recorded two birds calling close together; rarely did we find more than two birds in any 100 by 600-meter section, and the few we did find were always well spaced. Another basic assumption is that the areas not directly sampled are similar to the central regions where we did most of our work.

With these variables in mind, the total Guanica population probably ranges from 330 pairs, based on an average of one pair per 6.9 hectares, to 470 pairs, based on an average of one pair per 4.9 hectares. Because we considered low counts, the lower average is probably too low; and because we may have recorded singing females and all habitats were not optimal, the maximum may be too high. We feel the real population lies between these extremes and round our estimate to 400 breeding pairs.

The overall density of calling European Whip-poor-wills *(Caprimulgus europeaus)*, a bird of more open woods, has been determined for two environments in Europe: Lack (1932) found one pair per 6.9 to 8.1 hectares in sandy heath in England; and Schlegel (1967) found one pair per 9.7 to 10.3 hectares in Scotch pine-heather association in Germany. However, Schlegel also determined that individual pairs occupied five hectares, and, in some areas, overall densities reached one pair per 5.15 hectares. The Puerto Rican Whip-poor-will with one pair per 4.9 hectares shows very similar densities, holding slightly smaller areas than the European birds. It is tempting to speculate that the spatial needs in this genus are similar, but unfortunately we know too little about them. The European data do suggest that the Guanica birds may be at maximum possible densities within their limited range.

### Susua Commonwealth Forest

*General Description of Forest.* — Susua is a 1,300-hectare reserve of steep, rounded hills lying on the southwestern flanks of the Cordillera Central (Figure 8). Because it is closer than Guanica to the central mountains, it receives approximately 1,500 mm of rain per year, with more falling on the upper, northern slopes. Elevation ranges from 100 to 430 meters. The entire forest grows upon decomposed serpentine soils and, like the Guanica Forest, is not virgin. Most of the slopes and hilltops are presently covered with xeric scrub similar in profile to that in Guanica. Two permanent streams bisect the reserve, supporting a lush riparian community composed primarily of *Clusia rosea* (Guttiferae) and an endemic spiny palm (*Acrocomia media*), interspersed with various introduced species (*Eucalyptus, Eugenia, Inga*), especially on the broader stretches in the Rio Loco valley (Figure 9). This community is normally less than 100 meters in width, and its canopy is about 10 meters high, rising to 20 meters or more in some *Eucalyptus* stands. Scrub, four to five meters high, predominates at distances of 50 or more meters from the streams and extends to the hilltops, where it becomes much denser. Susua in many ways represents a transition between the dry limestone forests of the coast and the cordillera forests above. Xeric-adapted birds, such as the Key West Quail Dove (*Geotrygon chrysia*), occur together with montane forest birds characteristic of higher elevations, such as the Red-necked Pigeon (*Columba squamosa*). The Puerto Rican Whip-poor-will occurs in small numbers.

*Distribution of Whip-poor-will.* — We made an initial reconnaissance trip to Susua Forest on 20 June 1969 and were surprised to hear two Whip-poor-wills far below the road in the vicinity of the Rio Peces and the Rio Loco (Figure 9). We established two census routes, one in the scrub on top of the major hill lying between the Rio Loco and Quebrada Grande, the other in the riparian forests of the former stream. In February 1970 we established two additional routes on the southern edges of the reserve. We conducted 12 censuses on these routes, during which we recorded 29 Whip-poor-wills in 13.8 km, or 2.1 per km. The greatest number noted at one time was 17 birds on 19–20 February 1970. As in Guanica, the number of calling birds varies with the season but the drop in numbers in Susua is more dramatic because the birds are fewer and more scattered (Table 4). No *noctitherus* were heard in

TABLE 3

Whip-poor-wills and Mockingbirds as Indicators of Habitat in Guanica Forest

| *Route number** | *Route name*** | *Habitat description* | *Number of Whip-poor-wills* | *Number of Mocking-birds* |
|---|---|---|---|---|
| 3 | West Road | Woodland fairly dense with general lack of grass or brush at ground level | 37 | 3 |
| 4b | Lower Tamarindo | Open, dry limestone woodland with *Agave*, grassy meadows, and weedy appearance | 7 | 19 |

*Corresponds to number on Figure 5.

**Each one kilometer route censused in February, May, July, and November.

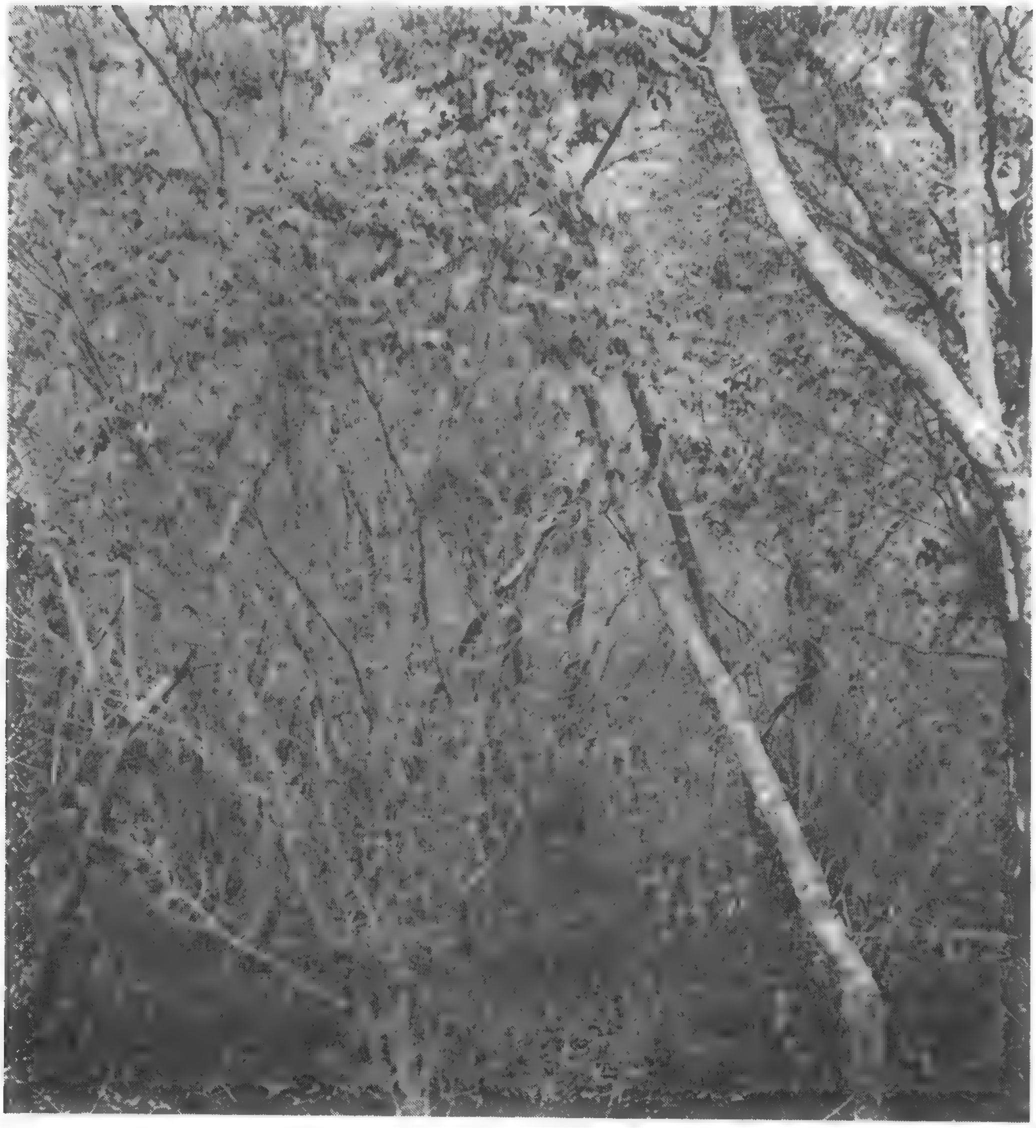


Figure 6. Vegetation profile in dry limestone forest where Whip-poor-wills are most abundant.

the riparian forests. The greatest numbers occurred in open scrub forests with horizontal visibility from five to seven meters; none were found in the denser sections where visibility dropped to three meters. This again suggests that density of cover is important. The thickets with limited visibility were choked, from ground level to canopy, with branches and small trunks that would undoubtedly hinder a flying Whip-poor-will.

*Population Density.* — We estimate that less than half, about 400 hectares, of the Susua Forest is suitable for *noctitherus.* If we assume that our February figures of 17 birds in 4.0 km represent real Susua densities, then each pair would require about 14.1 hectares, more than twice the area needed in Guanica. In fact, the distribution is patchy, reflecting the heterogeneous nature of the vegetation. Even so, the maximum densities within a limited area on the Pecos Trail were one pair per 12 hectares. This suggests that Susua is suboptimal habitat. Using our census figures, we estimate that the total Susua population is approximately 30 pairs.

### Guayanilla Hills

We discovered a third population in the limestone hills lying 8 km east of Guanica, 2 km from the coast, and 10 km west of the city of Ponce, the second largest city in Puerto Rico (Figure 5). The hills are surrounded by

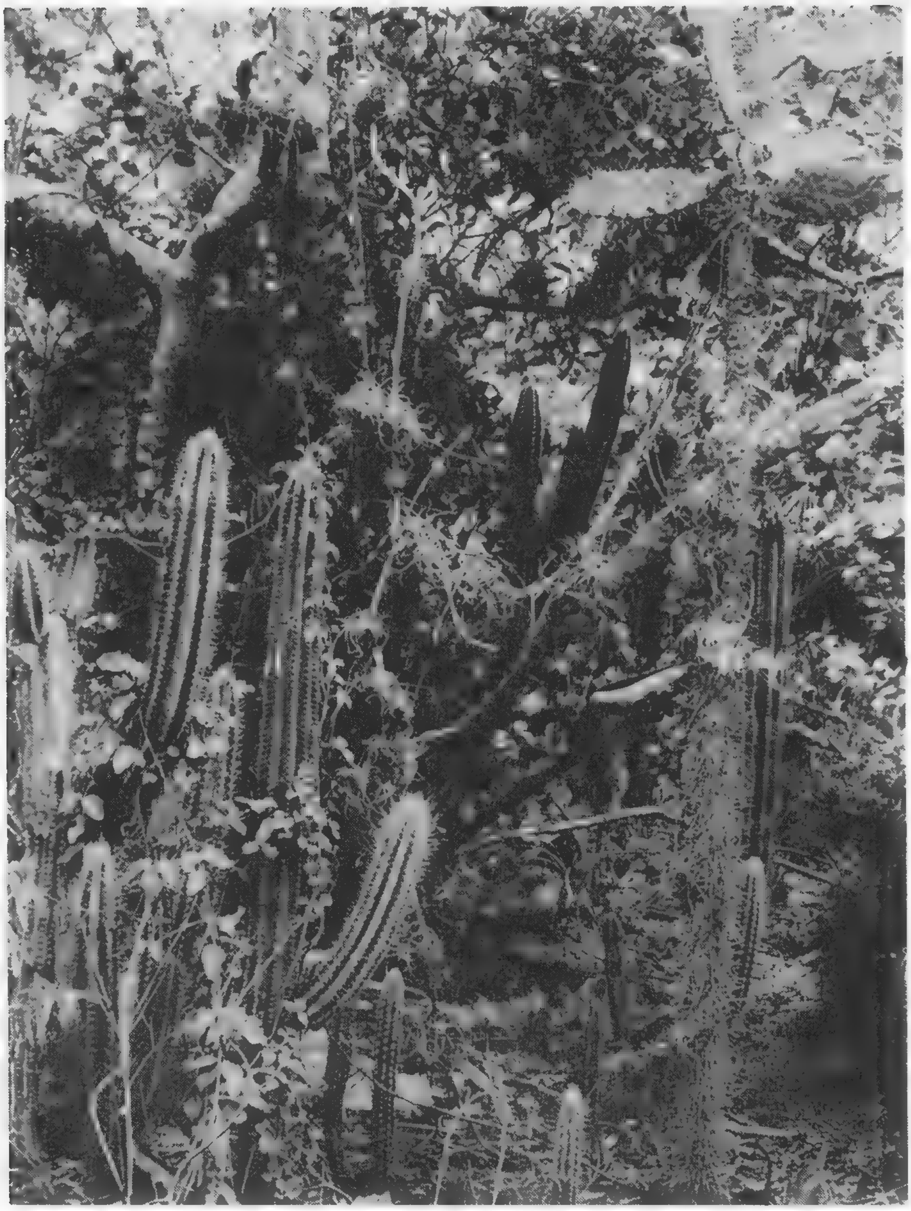


Figure 7. Vegetation profile in cactus forest where Whip-poor-wills are uncommon.

agricultural lands on the north, east, and west, and by a major highway, Route 2, in addition to a massive oil refinery on the south. The elevation ranges from sea level to 250 meters, and the vegetation is similar to that in Guanica. We made no detailed study in the area, but we heard three Whip-poor-wills from Route 2 before dawn on 11 July 1969. From topographic maps and a general survey, we estimated that the forest included approximately 500 hectares of suitable habitat. That the population could be fairly dense in this region is indicated by the Guanica-like habitat, the lack of water, and the concentration of calling birds near a major road at a time of year when calling is minimal. If densities are equal to those in Guanica, the population could approach an upper limit of 100 pairs. We conservatively estimated about 50 pairs for the region.

## Total Population Size

In summary, the world's only known populations of *Caprimulgus noctitherus* are restricted to three small areas, totaling approximately 3,200 hectares, each within 10 km of another. We estimated that the total population ranged from 450 to 500 breeding pairs and that 80 per cent of these occurred in Guanica Commonwealth Forest.

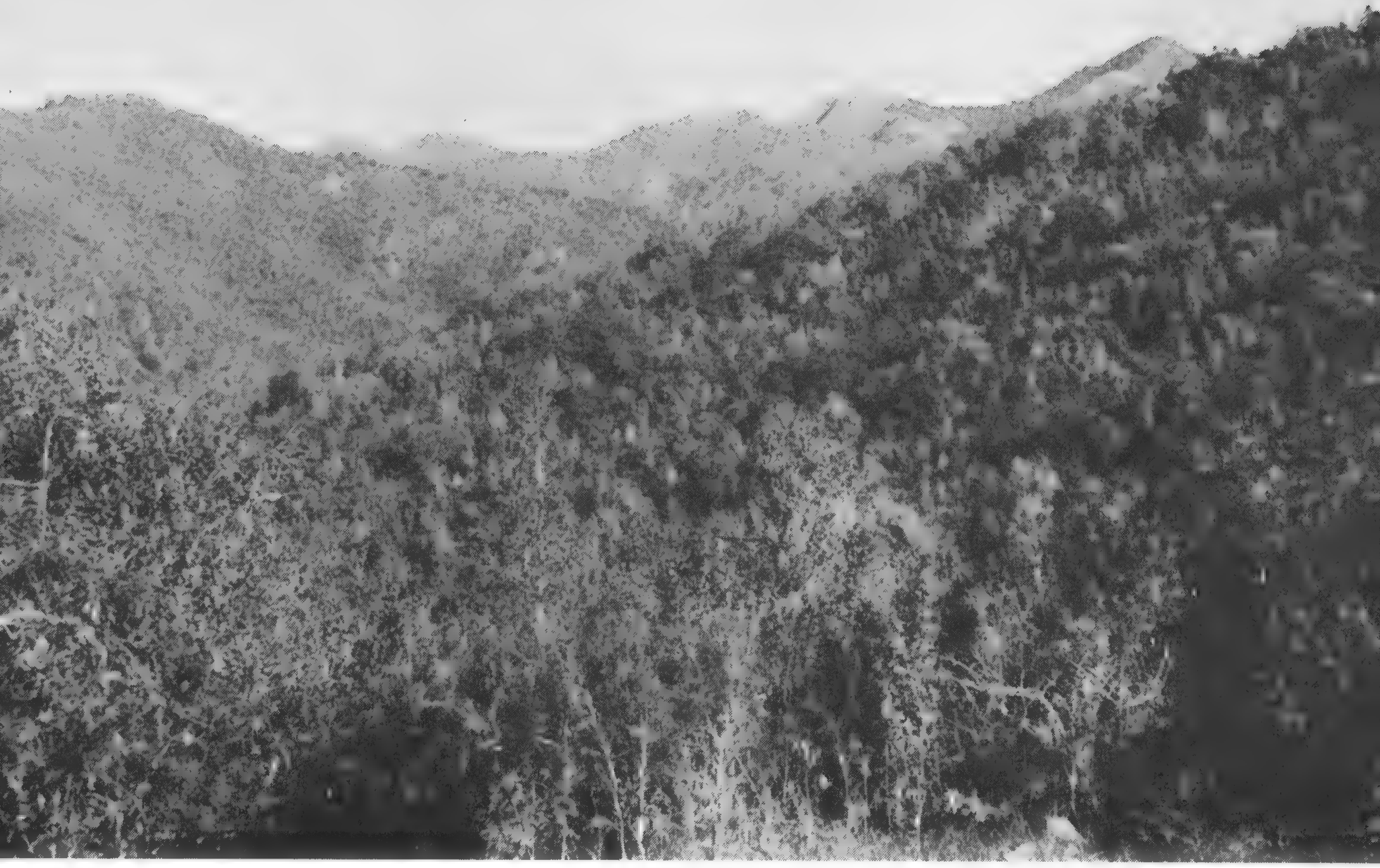


Figure 8. Susua Commonwealth Forest, showing the hilly nature of the reserve and the scrub forest characteristic of the lower half where Whip-poor-wills occur.

## *Vocal Behavior*

Reynard (1962) described the call in this species as a regularly repeated *whip* note showing a broader frequency range, from 1,200 to 2,200 cycles, than the first *whip* note of *C. vociferus,* from 1,500 to 2,000 cycles. Normally, the bird gives short irregular sequences of two to 15 calls, each followed by pauses of variable lengths. We found that, like other *Caprimulgus,* the Puerto Rican Whip-poor-will may deliver very long call sequences. In December 1970, one bird called more than 154 times without a break, paused three minutes, then gave 40 to 50 more calls. We never heard a bird give only one *whip.* We also found, as did Reynard, that one bird's vocalizations normally elicited responses from nearby individuals.

*C. noctitherus* calls all through the year, the nocturnal activity varying greatly with the amount of light. Calling is most frequent after dusk and before dawn and, as would be expected, the timing depends on the season although at this latitude, 18° 00′ N, variation in day length is small (Figure 10). The amount of light at night also affects calling, which is retarded if it is too bright with a full moon and no clouds or too dark with no moon and heavy clouds. We could not use October censuses because a nearly full waning moon was still bright at dawn, and we heard no calling. As a rule of thumb, if there is enough light to read by, *noctitherus* does not call.

TABLE 4

Summary of Whip-poor-will Censuses, Susua Forest

| *Date* | *Census trails** | | | |
|---|---|---|---|---|
| | 1. *Pecos Trail (1.0 km)* | 2. *Hi-wire Trail* | 3. *Hill-top Trail (1.5 km)* | 4. *Rio Loco Trail (0.9 km)* |
| 19 February 1970 | – | – | 5 | 0 |
| 20 February 1970 | 5** | 7 (1.5 km) | – | – |
| 10 December 1970 | 3 | 5 (1.0 km) | – | – |
| 29 May 1971 | 2 | 1 (1.5 km) | – | – |
| 27 July 1970 | 0 | 1 (1.0 km) | – | – |
| 9 July 1969 | – | – | 0 | 0 |

*Numbers for the census trails correspond to those shown in Figure 9.

**Numbers in columns indicate birds seen.

Superimposed on the above pattern is an annual variation in the number of individuals giving calls. There is a definite drop in calling in July compared with calling rates earlier and later in the year (Figure 11). This drop occurs during the breeding season, when adults are nesting, and may last into November. Thereafter calling increases and remains at high levels at least until late May. Unfortunately, no June records are available from Guanica, but the decrease probably occurs early in that month; it drops in late May in nearby Susua Forest (Table 4). It is important to note that, although calling is less, some birds do continue to sing during the breeding season, perhaps indicating a small population of birds that breed late or have a second clutch.

## *Breeding Biology*

There is no published information on the timing of the breeding season or the breeding biology of the Puerto Rican Whip-poor-will. During the present study we found two nests in Guanica and received some information on a third. This, together with helpful comments by the forest rangers in Guanica and Susua and our own observations of vocal behavior, provide a reasonably clear picture of the general nature of the Whip-poor-will's breeding biology. In all respects for which we have data, *Caprimulgus noctitherus* is very representative of its genus.

### Nest Dates and Breeding Season

We found one nest, on 18 June 1969, with two chicks, estimated to be 14 or 15 days old by using Lack's data for *C. europaeus* (1930a). The Guanica forest ranger showed us a nest with two eggs on 1 May 1971; the eggs hatched on 4 and 5 May. McCandless (pers. commun.) found a nest with one egg on 1 July; it contained two eggs on 3 July, and he assumed that the female began laying the day of its discovery. McCandless reported that incubation took 19 days, a figure typical for the genus (Table 5). Thus, incubation in our June nest

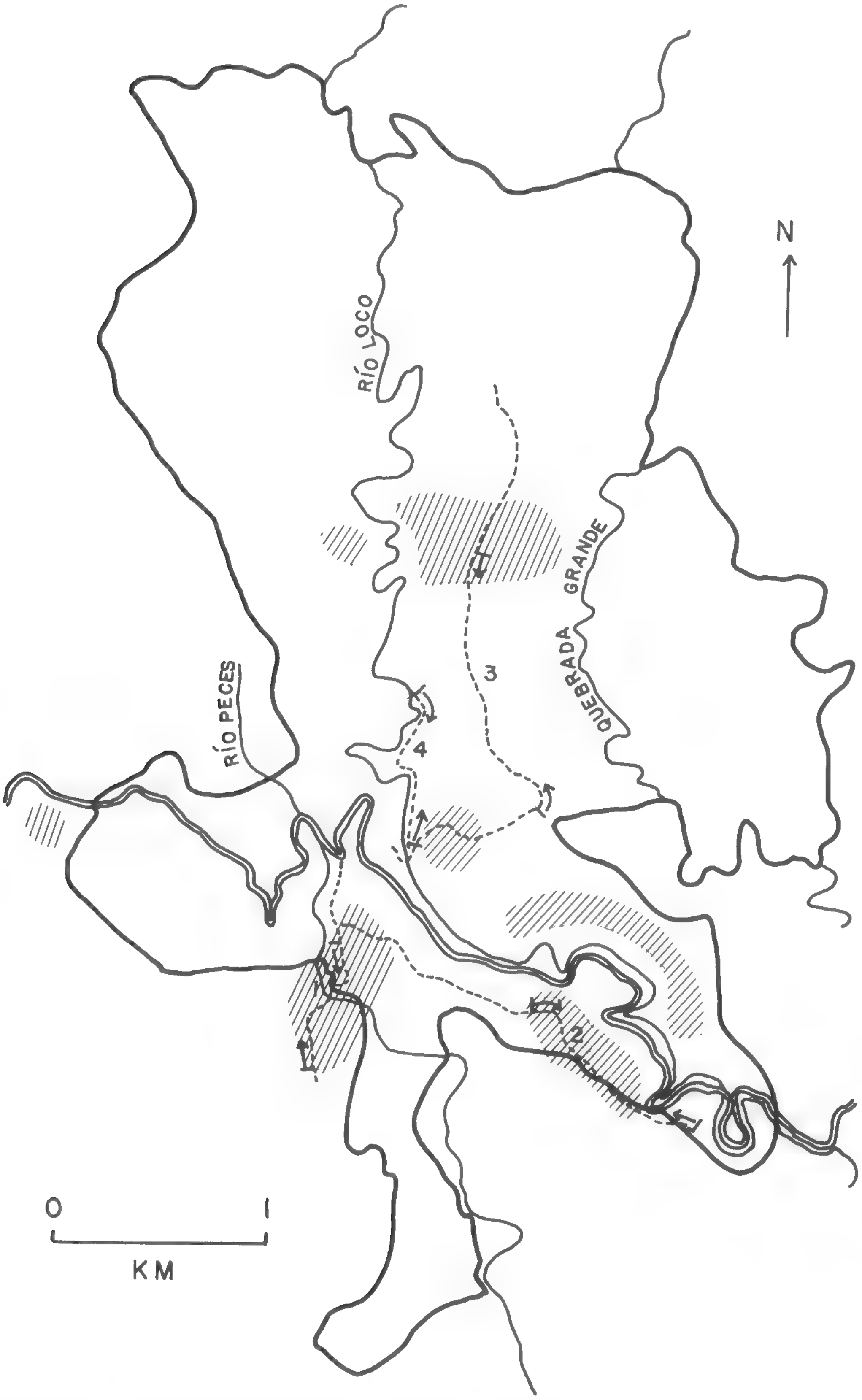


Figure 9. Map of Susua Forest. Diagonal lines show locations of Whip-poor-wills; numbers indicate census routes and correspond to routes listed in Table 4.

probably started on 18 or 19 May; and in the May nest on 16 or 17 April. The known dates, then, fall in a three-month period, mid-April through early July. The forest ranger at Guanica, who has a keen eye for nests of any kind, mentioned that eggs and young are always found in May and June, which probably represents the peak of nesting. In Guanica, Whip-poor-wills maintain a period of peak calling from February to May, with very low numbers calling in July. Calling in Susua shows a sharp decline in late May. Hoyt

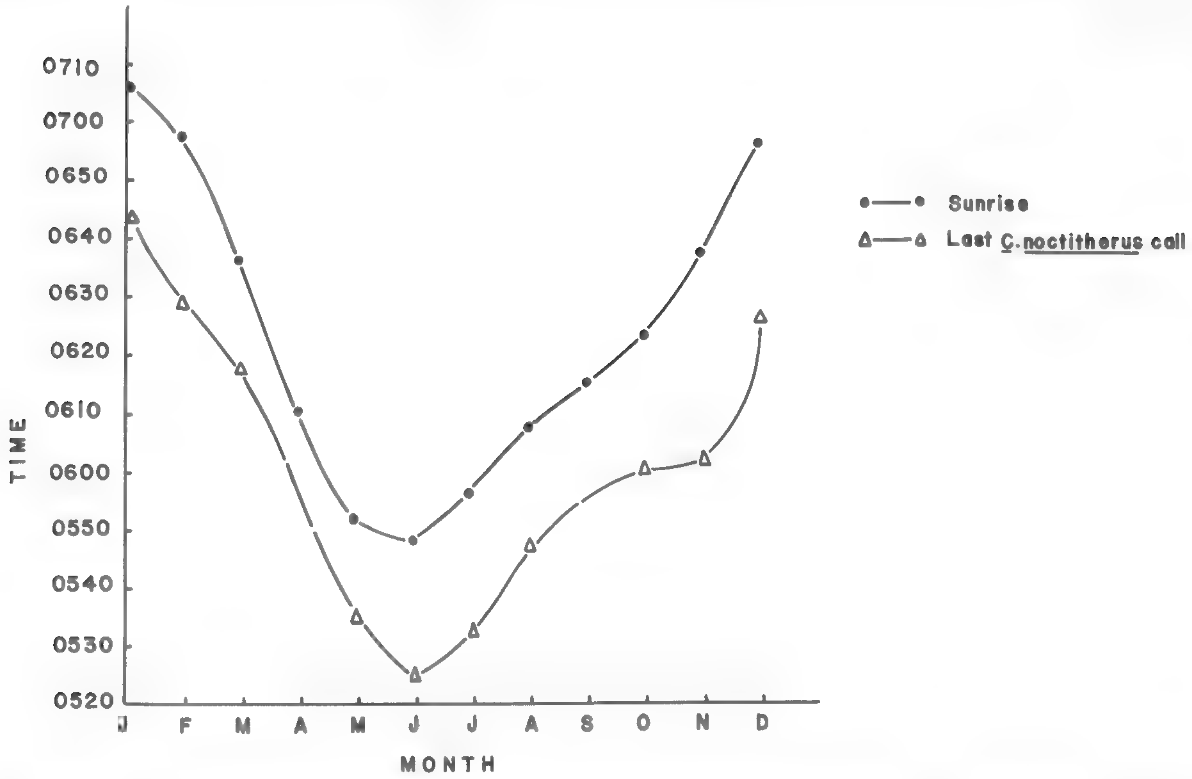


Figure 10. Annual variation in the time of last dawn calls, Guanica Forest. Sunrise times are from Her Majesty's Nautical Almanac Office, 1967 and 1968.

(1953) showed that in the Chuck-will's-widow (*C. carolinensis*) calling dropped markedly when the chicks hatched, and this should occur in *noctitherus* as well. Thus the drop in calling activity in Guanica (Figure 11) and Susua (Table 4) may represent the period when most adults have chicks.

Lack (1930b) demonstrated that *C. europaeus* has two broods a season in England; and this is suspected in Russia (Dement'ev *et al.*, 1966). There is also a suggestion that the Common Nighthawk (*Chordeiles minor*) has two broods (Weller, 1958), so the two "best-studied" (Rohwer, 1971) members in the family Caprimulgidae show this behavior. Without strong supporting evidence, we can only suggest that a breeding season of at least three months, sustained calling during the breeding season by some males, and new nests after peak calling has stopped may indicate that *noctitherus* also has two broods.

## Nest Site

The Puerto Rican Whip-poor-will does not construct a nest; the female merely lays the eggs directly on supporting leaf litter (Figure 12), under scrub vegetation, where the canopy ranges from four to six meters, and never in open areas or clearings. In the only "nest" we saw with eggs, the May nest, the eggs rested on bare litter 15 centimeters from the base of a tree that was approximately 10 cm in diameter. The site was partly open to the sky, with sunlight filtering to the ground, and horizontal visibility was approximately eight to 10 meters. There were few obstructions in the immediate vicinity of the nest. After hatching, the young wandered away, leaving the original nest with broken eggshells and a small accumulation of excrement as the only evidence that the site had been used.

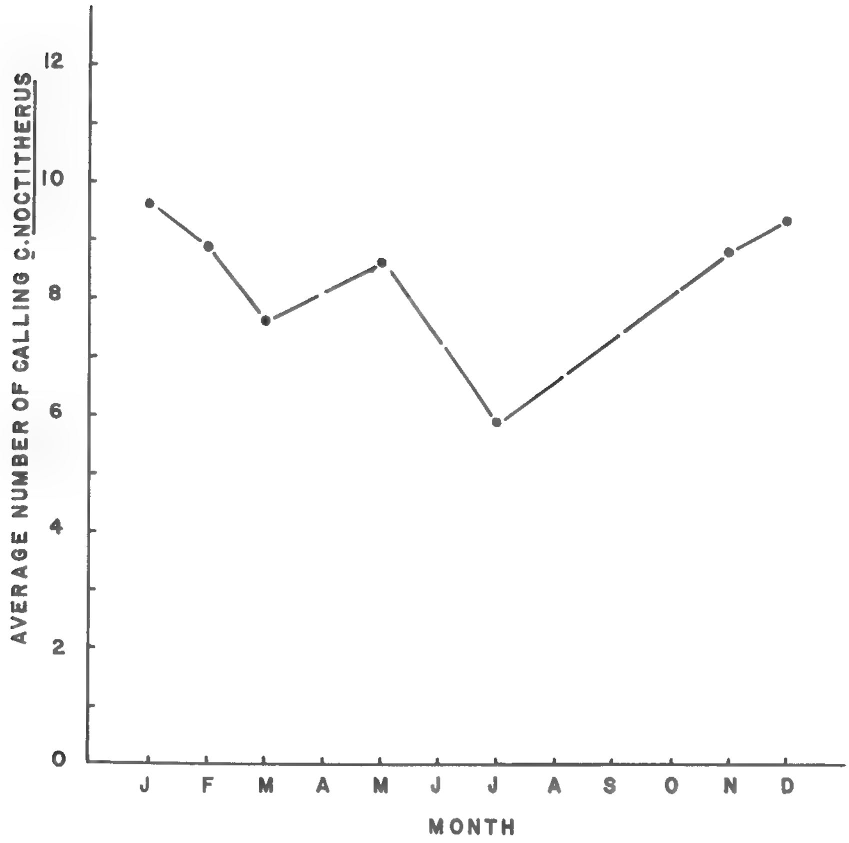


Figure 11. Number of calling Whip-poor-wills by month, Guanica Forest.

## TABLE 5

Breeding Data for Several *Caprimulgus* Species

| | *Species* | | | |
|---|---|---|---|---|
| | *noctitherus* | *vociferus* | *carolinensis* | *europaeus* |
| Clutch size | 2 | 2 | 2 | 2 |
| Laying period (days) | 1 | 1 | 1 | 1–2 |
| Incubation period (days) | 19 | 19–20 | 20 | 17–19 |
| Hatching | asynchronous | asynchronous | asynchronous | asynchronous |
| Weight of day-old chick (grams) | 5.1 | – | – | 5.8 |
| Nest movement | yes | yes | yes | yes |
| Age at first flight | 14 | 15 | – | 15 |
| References | Kepler and Kepler | Kilham, 1957<br>Tyler, 1940 | Hoyt, 1953<br>Sprunt, 1940 | Lack, 1930a, 1930b, 1932, 1957<br>Dement'ev *et al.*, 1966 |

## Eggs

The clutch, so far based on only three nests, is two, a number nearly universal in *Caprimulgus.* The buffy-brown eggs have numerous brownish purple spots of variable shape over the entire surface, coalescing into an irregular ring around the rounded end (Figure 12). This contrasts with the eggs of *C. vociferus,* which are pure white or occasionally faint creamy in base color (Tyler, 1940). The eggs are only moderately cryptic on the substrate, and depend upon the behavior of the incubating adult for protection against predators (Figures 13 and 14).

In McCandless' nest and in our May nest the eggs hatched one day apart. The young in the June nest showed pronounced plumage differences and an 11 per cent difference in wing length, 7.0 against 7.9 cm, flat, again suggesting hatching on successive days. Incubation begins with the first egg and takes 19 days (McCandless, pers. commun.). In all these characters *C. noctitherus* is a typical *Caprimulgus* (Table 5).

## Downy Young

The two downy young we observed between the day of hatching and two days of age were entirely reddish buff or cinnamon, similar to the "pinkish-cinnamon" described for young *C. vociferus* (Tyler, 1940). The toes and legs were flesh-gray, with the bottom of the feet pearl. The iris was dark brown, bill brown, and gape pink. Weights and measurements of the two chicks are given in Table 6. The eyes were open on the day of hatching, and the egg-tooth remained on the two-day-old chick. We collected the first chick on its second day (USNM 511684).

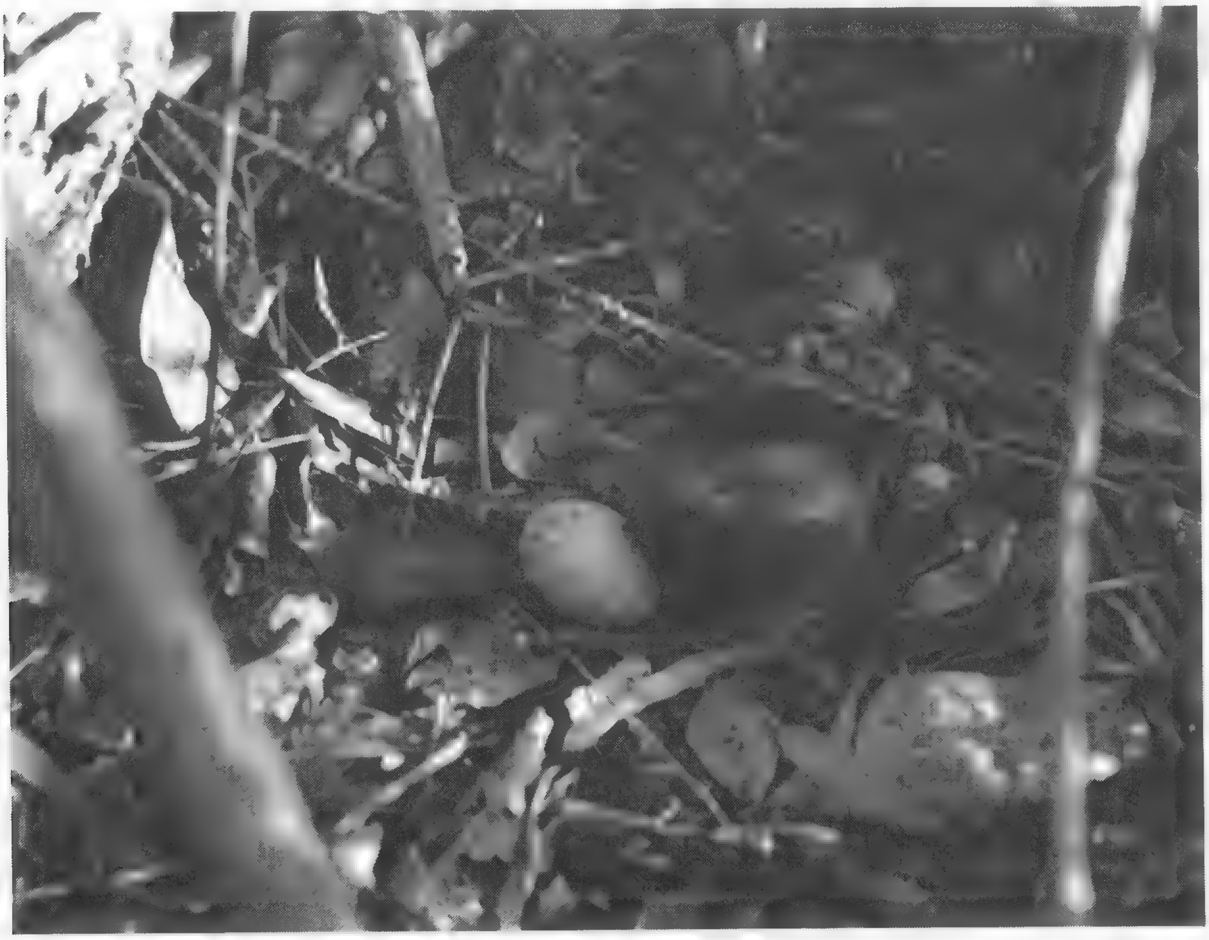


Figure 12. Puerto Rican Whip-poor-will nest with one egg and one chick in Guanica Forest, 4 May 1971.

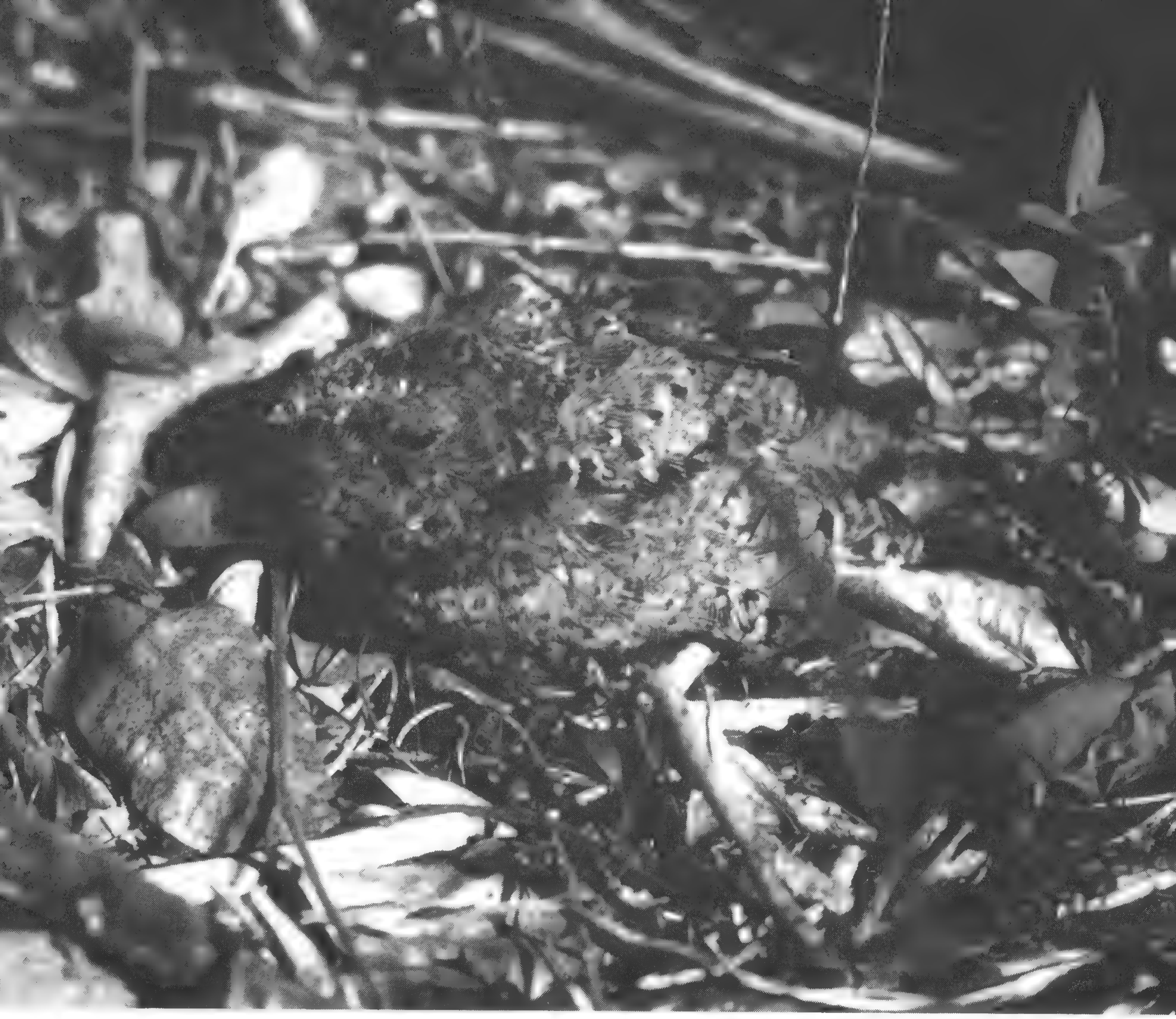


Figure 13. An immature Puerto Rican Whip-poor-will in Guanica Forest, 18 May 1969.

## Nest Attendance and Movement of Young

Lack (1932) and Tyler (1940) found that during the day only the female incubates in *C. europaeus* and *C. vociferus*, respectively, while the male normally roosts "50 to 100 yds" from the nest (Lack, 1932). Only once did we see two birds near a nest; on 1 May, four days before the first egg hatched, a Whip-poor-will, perhaps the male, flew up three meters from the nest, as we arrived, while another bird remained on the eggs. We never saw a second bird again, nor did we find a second adult near the chicks that we discovered in June 1969, so it presumably roosted some distance away.

Many authors have noted that young caprimulgids regularly move from the nest site at an early age (Table 5; Rust, 1947, for the Common Nighthawk; Skutch, 1945, for the Pauraque, *Nyctidromus albicollis*; and others), and Kilham (1957) described the movement of eggs by the adult. When we left Guanica on 5 May, Sr. Ricardo Cotte, who was involved in the rediscovery of the Whip-poor-will (Reynard, 1962) and was studying doves in Guanica, continued to check the nest each day to observe any movement by the remaining chick. He reported that its first move, of 20 cm, occurred on the third day and that it

### TABLE 6

Weights and Measurements of *C. noctitherus* Chicks*

| | *Chick No. 1* | | *Chick No. 2* |
|---|---|---|---|
| | *One day old*** | *Two days old*† | *One day old*** |
| Weight (gr) | 4.15 | 5.81 | 4.16 |
| Wing (mm) | 7 | 11 | 7 |
| Tarsus (mm) | 8.5 | 11 | 8 |
| Middle toe (mm) | 9 | 11 | 9 |
| Eyes | open | open | open |
| Egg-tooth | present | present | present |

*Data collected in the Guanica Forest, 4–5 May 1971.

**One day old equals day of hatching.

†Chick collected, USNM 511684.

moved irregularly thereafter (Figure 15). The chick was capable of considerable movement and sustained flight by Day 14 when it showed the adult plumage pattern. One adult remained with the chick at least until Day 14, the last time he saw it.

## Distraction Display

The incubating bird remains on the eggs even when closely approached — we took several photographs of it while standing less than one meter away. This behavior is necessary because the eggs are conspicuous against the leaf litter and easy to detect if left exposed. The behavior of the non-incubating bird on 1 May, if normal, is also highly adaptive in that a potential predator would be most likely either to pursue the bird or search the area from which it flew, leaving the nest behind. If approached very closely, however, the adult will leave the eggs and fly off. The display the adult gives varies greatly with the circumstances, as it does in other species (Lack, 1932; Gramza, 1967). Below we have described the distraction displays that we saw:

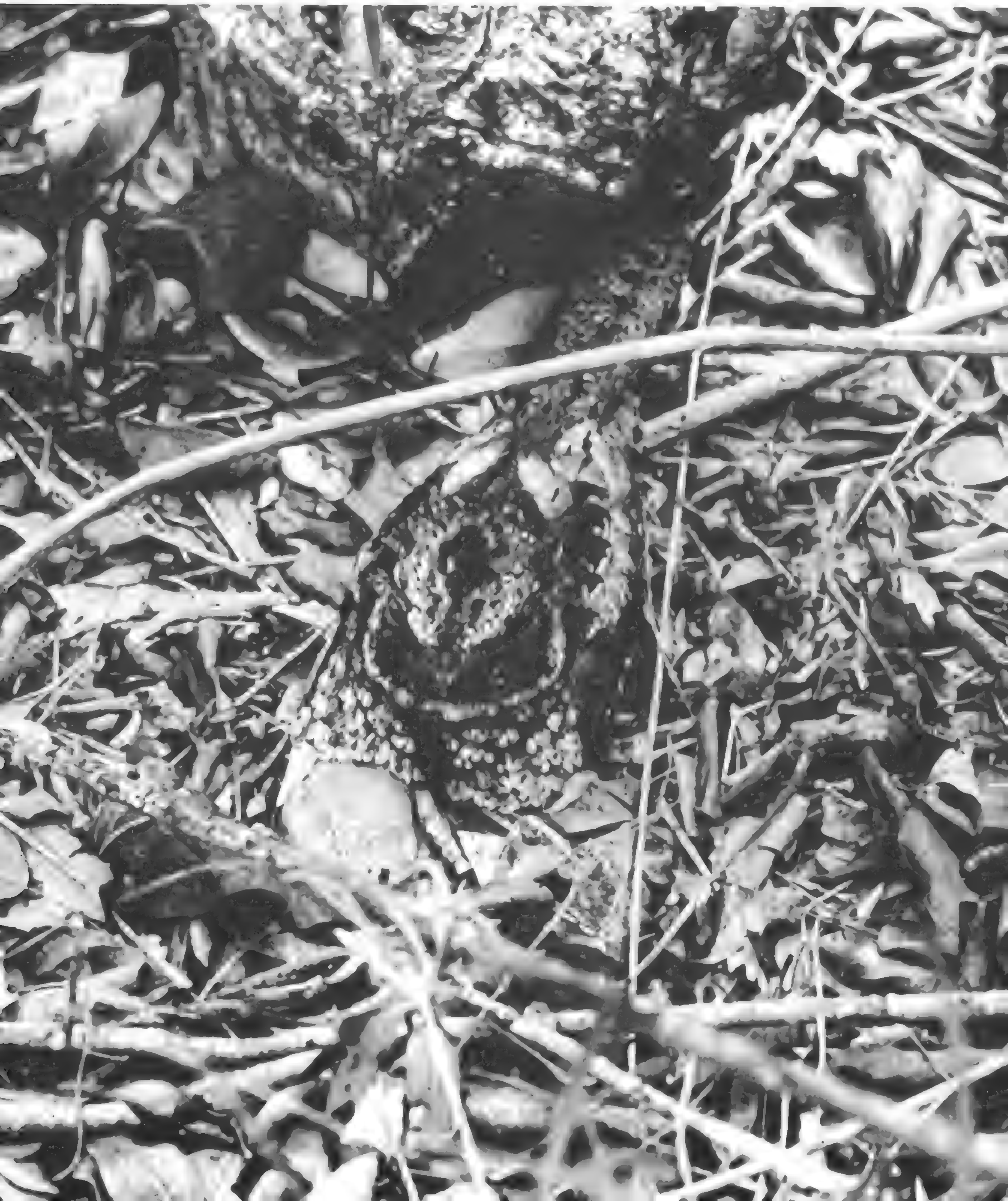
On 1 May 1971, an adult, with eggs incubated about 15 days, responded to the camera flash by flying up in a parabolic arc and landing on the ground two meters beyond the nest and away from us. It spread its wings and tail widely, showing the very prominent white tail patches; it gave no loud vocalizations. Then quickly it flew two meters farther away and remained there without further display while we photographed the nest.

On 4 May at 12:22, an adult with one chick repeated the pattern when we checked the nest, except that, on landing, it fluttered its wings against the ground, and spread the tail against the ground. It gave no vocalizations.

Later the same day, at 17:30, the adult flew silently when we approached to within two meters and landed five meters away, facing us. After landing, the bird fully extended the wings, vibrated them rapidly, and spread its tail, exposing the white patches. Its eyes were fully open, and its bill was open wide but the bird did not snap it nor did it give any vocalizations. When we went closer, the bird flew deftly through the scrub, hovering momentarily and landing again on the ground. Now broadside to us, it spread its wings again and vibrated them through an arc of less than one cm at the tips. The tail was spread and the bill open. Several seconds later, it flew from our sight. We left the area, and when we returned 15 minutes later, the adult was 0.8 meter from the nest.

On 18 June 1969 at 16:00, we found an adult with two chicks estimated to be approximately 14 days old. The adult flew up when we were within one meter, and flew slightly more than one meter, landing on a branch. It then flew to the ground, leaping almost immediately to a second branch, where it remained for more than 10 minutes (Figure 16). On the first branch, the bird drooped its wings extensively, opening and closing the bill rapidly to reveal an enormous pink gape. It did not snap its bill, but gave a loud call. In flight, the wings appeared to be held in a strong V position, especially just before landing. On the ground the wings were extended horizontally and vibrated rapidly. The bill opened and closed rapidly with audible snaps accompanied by a raspy growl. On each flight, the bird moved directly away from us before displaying.

Figure 14. Incubating Puerto Rican Whip-poor-will, showing nest location and character of the nest site in Guanica Forest.



David Lack was with us during our last observation of the distraction display and remarked that, in all phases, it was remarkably similar to that of *C. europaeus* (Lack, 1932). This behavior is extremely effective in creating a conspicuous object near a predator and away from the nest. The bold white tail patches and pink gape, looking like a wound, are enhanced by wing-flapping on the ground and the V pattern before landing.

Gramza (1967) found that flushing distances in the Common Nighthawk were shortest and that the display was most intense shortly after hatching, presumably when the young are most vulnerable; this differed in *noctitherus*, whose most intensive displays appeared when the chicks could fly short distances.

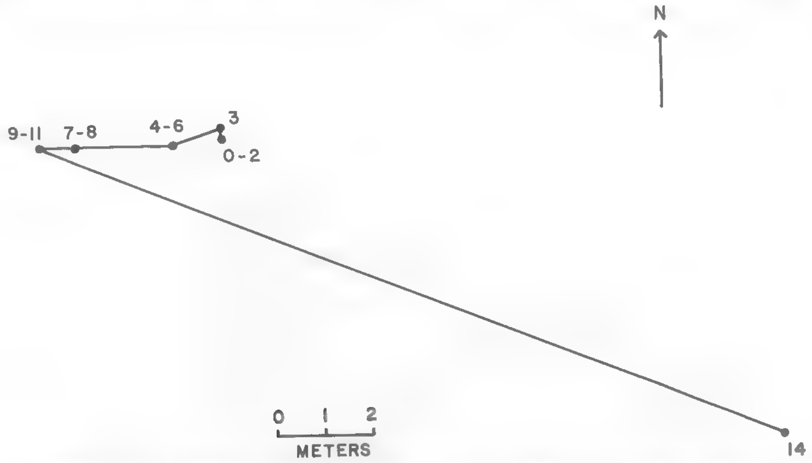


Figure 15. Daily movement of young Puerto Rican Whip-poor-will from original nest site. Numbers are the age of the chick in days.

## Perching and Roosting

Like *C. vociferus, C. noctitherus* is a bird of the scrub forest and undergrowth. We always saw it within the cover of vegetation, often near its edge, and with the exception of the bird described below, we found nonbreeding birds perched at night only eight times. Of these, one was on the ground in a brushy trail, while the others were perched, either crosswise or along branches normally greater than one centimeter, from three to six meters high near the canopy. When disturbed they flew adroitly through the branches with the traditional "mothy" flight and V-shaped wing position. These birds were all within one meter below the canopy top and did not fly above the emergent trees.

Tyler (1940) noted the regularity with which *C. vociferus* visits favorite perches night after night as it feeds. Although we could not watch this ourselves on our short trips to Guanica, the forest ranger assured us that *noctitherus* behaves similarly, and that one bird came to a tree in his yard each evening to feed. We watched the tree from 1 to 4 May 1971, and the bird arrived and called each night. Cotte watched the tree in our absence. From 5 to 22 May, the bird appeared and sat in the upper branches between 19:30 and 22:15 on all but three nights; since two of the nights were very dark, Cotte could have overlooked it. The observations of the ranger and Cotte indicate that *noctitherus* probably has favorite perches that it uses regularly. The bird always landed in the top third of the tree, four to six meters high, and sallied out after insects. We failed to see this, but all the sightings above suggest that the bird captures most of its food by sallying from perches well above ground. The wings of *noctitherus* are proportionately shorter in relation to its tarsus

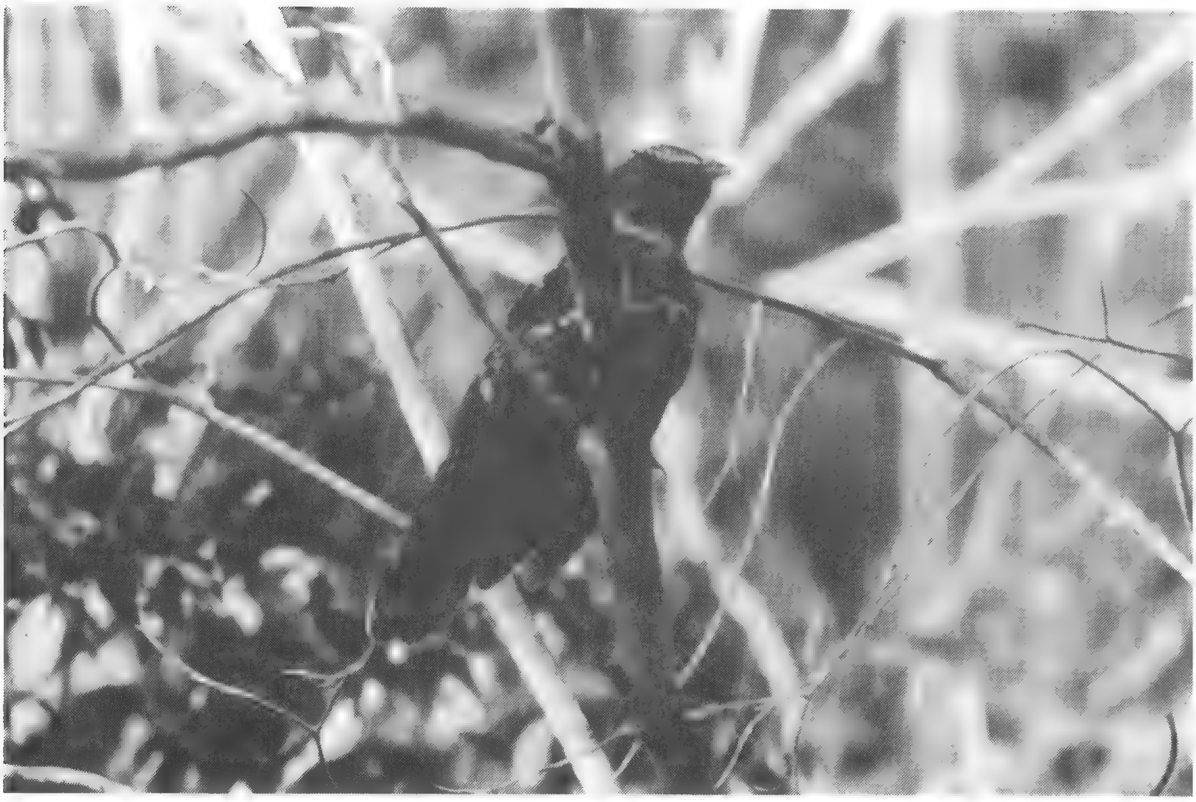


Figure 16. Puerto Rican Whip-poor-will perched on horizontal branch after flushing from two nearly fledged chicks.

and tail and absolutely shorter in length than those of *vociferus* (Ridgway, 1914), which feeds by sallying (van Rossem, 1927; Tyler, 1940), and *europaeus,* which feeds mainly in continuous flight (Witherbee *et al.,* 1938; Lack, pers. commun.). This difference is more pronounced between *noctitherus* and the West Indian Nighthawk (*Chordeiles gundlachii*), which spends even more time feeding in flight, as described below.

## *The West Indian Nighthawk*

Eisenmann (1962) described the taxonomy of the West Indian Nighthawk, the breeding nighthawk in the West Indies, as "controversial"; and this is certainly the case. He cited a number of reasons for considering the bird specifically distinct from the mainland form, the most important being its distinctive voice and sympatry with *Chordeiles minor* on Key Largo, Florida (Bond, 1963; Nicholson, 1957; Sutherland, 1963). Bond (1963) argued that even though both forms occurred on Key Largo and gave their characteristically different calls, there was no evidence of reproductive isolation because no incubating females had been collected. Monroe (1968) followed Eisenmann; and Mayr and Short (1970) asked for more data before changing the present taxonomic allocation (*C. minor gundlachii*). We find the opinions of Eisenmann more persuasive than those of Bond (1963, 1969), and treat the West Indian form as a Caribbean endemic, *C. gundlachii.* If anything, the sympatry in Florida, coupled with the smaller size and different coloration of the adults (Eisenmann, 1962), the very different vocalizations, and the clutch of one egg rather than two over most of its range (Bond, 1958; Lack, pers. commun.; Nicholson, 1957; Wetmore and Swales, 1931) provide more support for splitting this from *C. minor* than for splitting *C. noctitherus* from *C. vociferus.*

## Distribution

In Puerto Rico, *Chordeiles gundachii* is a summer resident primarily in the arid southwest although small numbers occur along the west coast and the limestone forests of the north; records exist from Bayamon and San Juan (Wetmore, 1927) so the range is nearly identical to the former range of *C. noctitherus.* At present its greatest numbers occur in southwestern Puerto Rico, and its range completely embraces that of *noctitherus.* We have found the nighthawk from Cabo Rojo (Figure 5) to Ponce, and extending from the coast to the lower cordillera at Susua. Within this region we have found birds foraging over shoreline, sugar cane fields, pasture lands, towns, and dry limestone and lower cordillera forest, so that we know it is a much more broadly adapted species than *C. noctitherus.* Because it breeds and forages in Guanica Forest, we became interested in the nature of the ecological separation between the two caprimulgids.

## Foraging Behavior

*C. gundlachii* hawks insects in the air high above the vegetation by flying steadily, swerving erratically, and diving steeply in pursuit of its prey. Like *C. minor* (Gross, 1940), it begins feeding well before dark, normally within one to two hours before sunset, although we once saw an individual in July feeding over Guanica at 16:20 when sunset was at 19:11. They are very active until dark, after which they normally stop calling, although they may continue to feed silently (van Rossem, 1927). They also have a brief period of calling and foraging at dawn. Normally, they remain above 30 meters or more, but may swoop to within 10 meters of the canopy on occasion; we never saw them enter the canopy. We found single birds or groups of two to three most frequently over Guanica Forest, and flocks of 20 to 30 birds twice over newly cut sugar cane fields to the north. In their feeding behavior they are separated completely from *C. noctitherus* in Guanica, foraging earlier in the day and at greater heights, and hawking insects on the wing rather than sallying from perches.

## Nesting

Nighthawks arrive in Puerto Rico in April, and by early May one hears their dives and booms in the Guanica Forest. Displaying continues at least until mid-July when we heard them every night and dawn for five days in 1969. We found three nests from 18 to 21 June 1969 and had a report of a fourth from Cabo Rojo during this period. Wetmore and Swales (1931) reported nests from May and June in Hispaniola, and David Lack and Peter Lack (pers. commun.) found three nests in June in Jamaica; the breeding season is probably similar on all the Antilles. In Guanica Forest, *gundlachii* and *noctitherus* breed at the same time of year.

All the nighthawk nests were on open patches of ground and lacked any cover or protection from the sun. One was beside the edge of the main asphalt road in Guanica, the second in the center of a dirt road, and the third on limestone "tableland" only 150 meters from the sea (Figures 17 and 18). The single egg rests directly on the gravel without any protecting leaf litter or other vegetation. All the eggs, pale gray and covered with fine scrawls and blotches of a slightly darker hue, were extremely cryptic against the substrate strewn with pebbles and small stones of irregular shape, with the broken field of pebbles greatly enhancing the disruptive color of the egg itself (Figure 18).

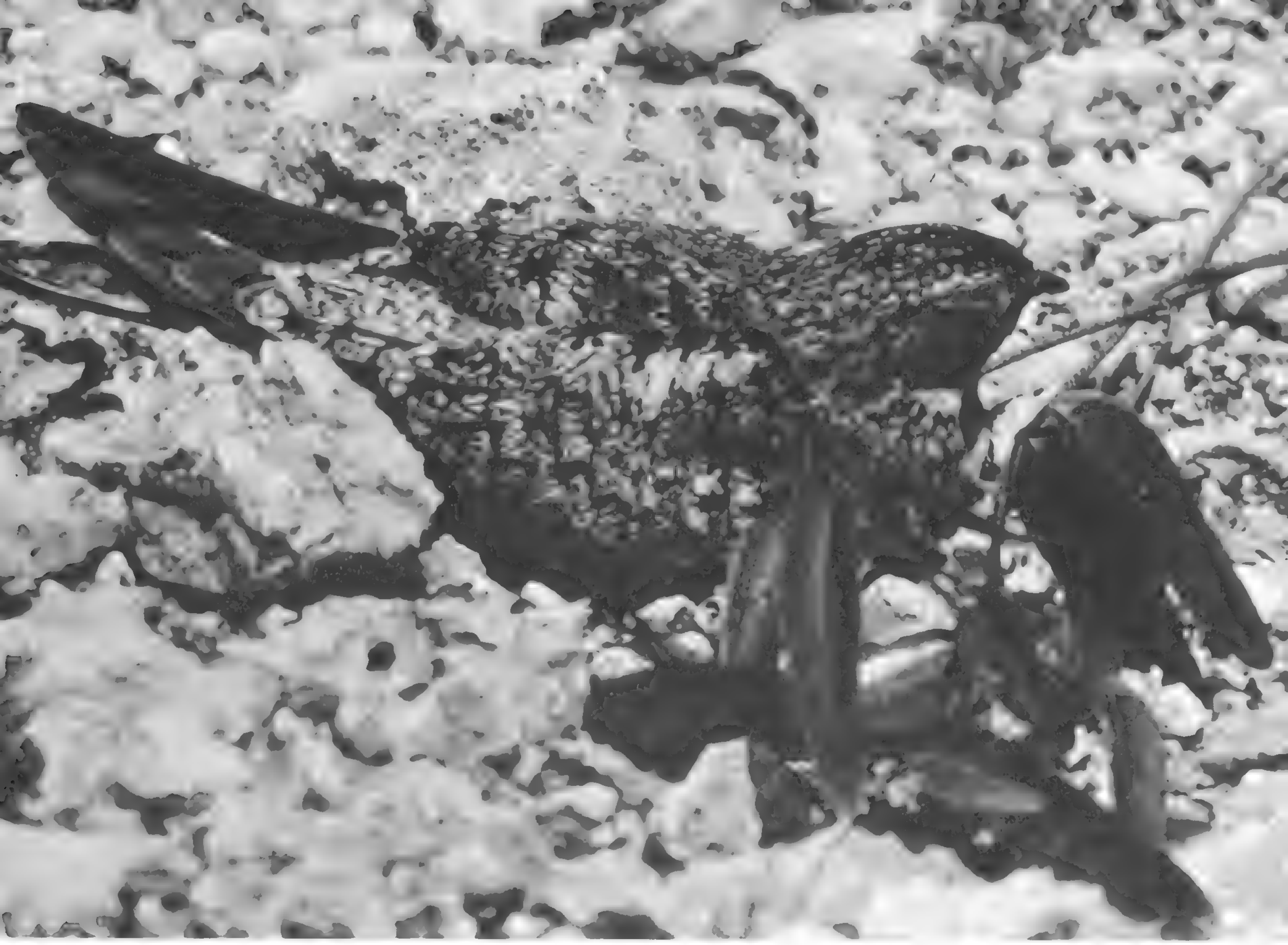
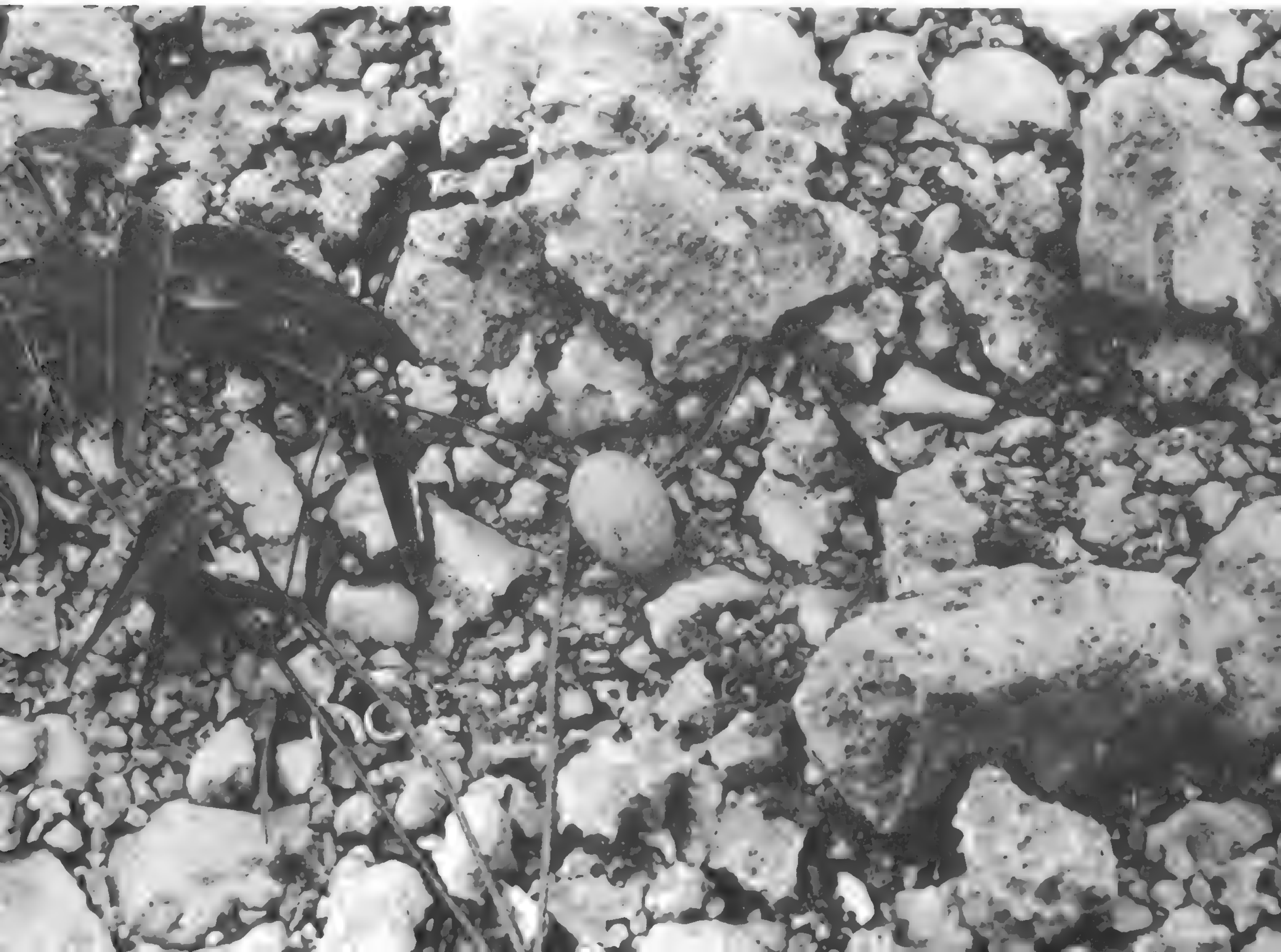


Figure 17 (*above*). West Indian Nighthawk incubating single egg in Guanica Forest, 20 June 1969. Note exposed nest site.

Figure 18 *(below).* West Indian Nighthawk egg, showing characteristics of the nest site.



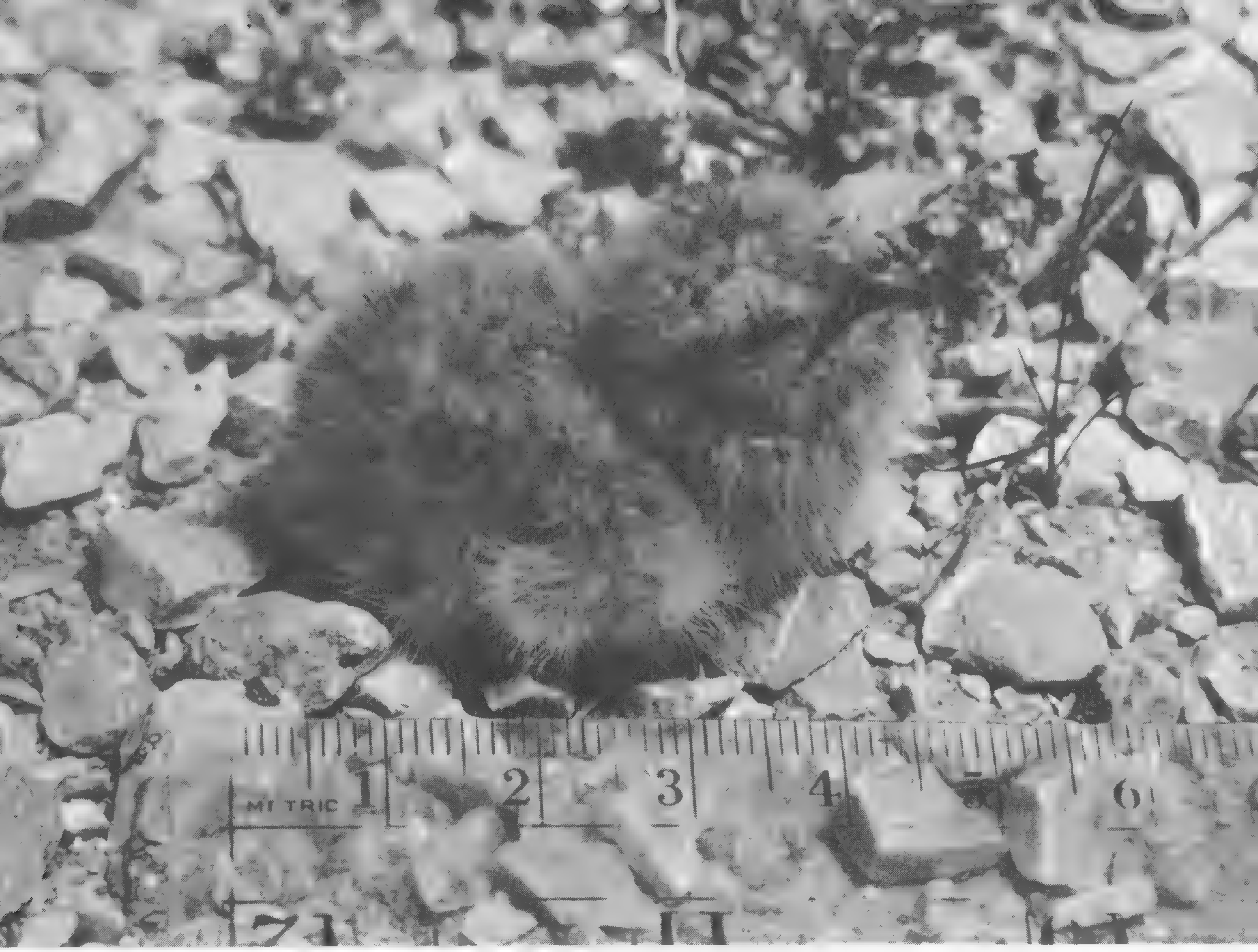


Figure 19. West Indian Nighthawk chick, one day old.

The incubation period is at least 19 days; the egg in a nest found on 21 June hatched on 10 July. The chicks are cinnamon-brown, without conspicuous markings (Figure 19). Their eyes are open and they begin wandering shortly after hatching — one moved 60 cm from the "nest" on its first day, 10 July. We found two of the three chicks in July, and both had moved from the nest site to the edge of their clearings, thus gaining some protection from the sun and becoming even more cryptic in the dappled shadows of the vegetation.

Two of the Guanica nests were above the 75-meter contour within the center of the range of *C. noctitherus*. However, each species chooses a very different nest site, *noctitherus* remaining within the cover of the limestone forest, *gundlachii* always selecting sites in the open. The man-made clearings within the forest reserve obviously have benefited the Nighthawk by allowing it to penetrate the range of the Whip-poor-will, but within this overlap zone there is no competition for food or nest sites between the two.

## *The Future*

Although the Puerto Rican Whip-poor-will is much more numerous and widespread than formerly believed, it is still an endangered species because its lowland range is threatened at the present time. Puerto Rico is developing rapidly, and the human population of 2.8 million — 320 per square km — is expected to double before the end of the century. Rapid growth throughout the island puts increasing pressure on the land, particularly in coastal areas. The region between Ponce and Guanica Forest is devoted to heavy industry. A huge and rapidly expanding petrochemical complex, primarily controlled by the Commonwealth Oil and Refining Company (CORCO), lies adjacent to the Guayanilla *noctitherus* population and only eight kilometers east of Guanica (Figure 20). Stack effluents from the complex blow across the privately owned and totally unprotected Guayanilla hills 24 hours a day with undetermined effects upon the vegetation. Fortunately, the Guanica and Susua Forests, as reserves, receive some protection from development and other disturbances. However, Guanica has been under various pressures during the past two years, and the possibility exists that it will not survive the mounting and unforeseeable threats. In 1969–1970, plans were formed for a copper smelter next to the Guanica Forest. Consequent effluents, including a heavy load of sulphur dioxide, would have blown directly across the hills harboring 80 per cent of the Whip-poor-will population. Conservation interests vigorously opposed this development, and the smelter site was relocated. Plans are being developed for the use of a valley within Guanica Forest as a "sanitary landfill" for the adjacent cities of Guanica, Yauco, and Guayanilla. This could destroy several hundred acres of the forest, and provide a food supply for rats and mongooses, which, in turn, could penetrate farther into the forest and prey on Whip-poor-wills. Industrial expansion to the east threatens the area as air pollution and the demand for additional land increases. Less than 10 km to the west, the Lajas Valley has tentatively been chosen as the site for Puerto Rico's second jetport; the pressures this could generate throughout the southwest are frightening to contemplate.

Unfortunately, the Commonwealth Forest system is not immune to industrial pressure. Over 400 hectares have been destroyed within the last five years by Puerto Rican Government-approved developments (Victor Ortiz, Chief, Commonwealth Forest System, pers. commun.); a large part of Aguirre Forest was destroyed for petrochemical development. If the Whip-poor-will is to survive, the government must protect the Commonwealth Forest system more rigidly, and make the Guanica unit an inviolable preserve for *noctitherus* and the other unique animals and plants that inhabit Puerto Rico's last good, dry, limestone forest.

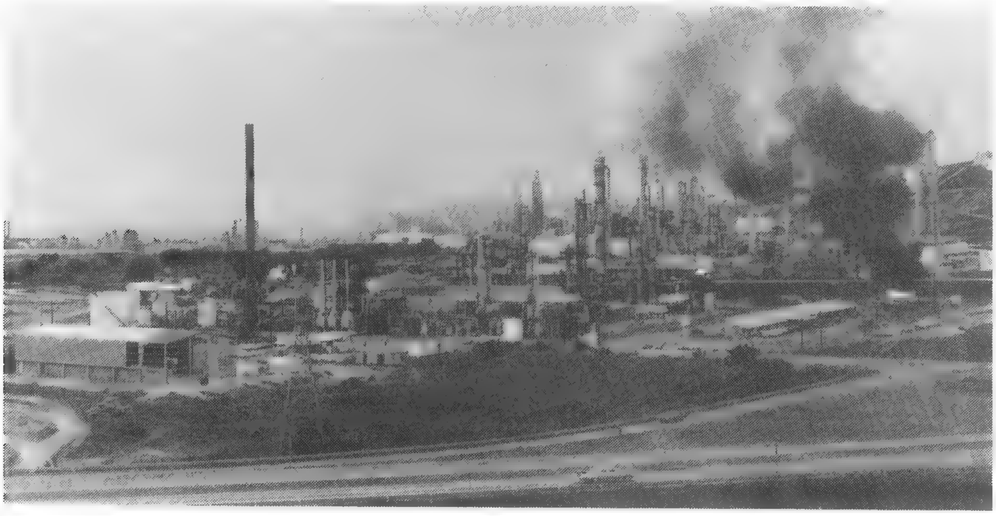


Figure 20. View of Guanica Forest and the Puerto Rican Commonwealth Oil and Refining Company (CORCO). Guanica lies behind the refinery and the Guayanilla hills slightly out of the photograph to the right.

## *Summary*

The Puerto Rican Whip-poor-will *(Caprimulgus noctitherus)* was considered extinct until its rediscovery in southwestern Puerto Rico by G. B. Reynard in 1961. Prior to 1969, when we began our three-year study, fewer than 100 birds were thought to exist in the Guanica Forest, the species' only known location. The species was included in the United States and International lists of rare and endangered species.

We began by censusing the Guanica population and searching for additional birds in 15 trips to southwestern Puerto Rico and other parts of the island. We located two additional populations in forests near Guanica.

The Whip-poor-will formerly inhabited all the limestone forests on the island, and probably beyond them on both north and south coasts. The Whip-poor-will presently inhabits 3,200 hectares, three per cent of its probable former range, and only 0.7 per cent of the total land surface of the island.

Some birds call all year in Guanica Forest, mostly at dusk and before dawn. The greatest numbers call from November through May; calling decreases during and following the breeding season.

*C. noctitherus* is irregularly distributed in Guanica Forest. The population centers on the higher slopes, above 75 meters, in the best semi-deciduous forest. The birds are rare or absent over most of the cactus-dominated forest below 75 meters, an area we consider unsuitable because of the preponderance of dense vegetation near the ground.

In the heart of its range, the maximum density was one pair per 4.9 hectares, a figure very close to densities found for *C. europaeus* in England and Germany. Approximately 2,300 hectares of optimal habitat exists in, and adjacent to, Guanica Forest, where we estimated the population at 400 breeding pairs. Susua Commonwealth Forest, 10 kilometers to the north, and the hills behind Guayanilla, eight kilometers to the east, support about 80 pairs. Thus, we estimate that the total known population stands at 450 to 500 breeding pairs, over 80 per cent of which occur in Guanica Commonwealth Forest.

The breeding season extends from April to June. The clutch size is two; eggs, laid on successive days, are placed on leaf litter on the ground; there is no constructed nest. Chicks hatch on successive days and begin wandering within four days. Two chicks weighed 5.1 grams each on the day of hatching. Distraction display, more pronounced when the adults have chicks, consists of wing-flapping, tail-spreading, gaping, and, at high intensities, bill-snapping and growling. In all respects, for which we have data, *C. noctitherus* is very typical of the better-studied members of its genus.

The West Indian Nighthawk (*Chordeiles gundlachii)* is broadly sympatric with *Caprimulgus noctitherus* and breeds in the same months in Guanica Forest. *Chordeiles* nests on bare stony ground in hot, bare clearings, and feeds by hawking insects on the wing well above canopy level, flying at times over agricultural areas. The Whip-poor-will, by contrast, nests under the cover of the forest, and takes insects by sallying from perches near, but below, the canopy within the forest. The two species do not compete for food or nest sites in their overlap zone.

Although Susua and Guanica Forests are nominally protected, the tremendous industrial expansion to the east and possible development to the west threatens them both. Until Guanica gains additional recognition and protection from the government as an inviolable preserve, the survival of the Puerto Rican Whip-poor-will remains in doubt.

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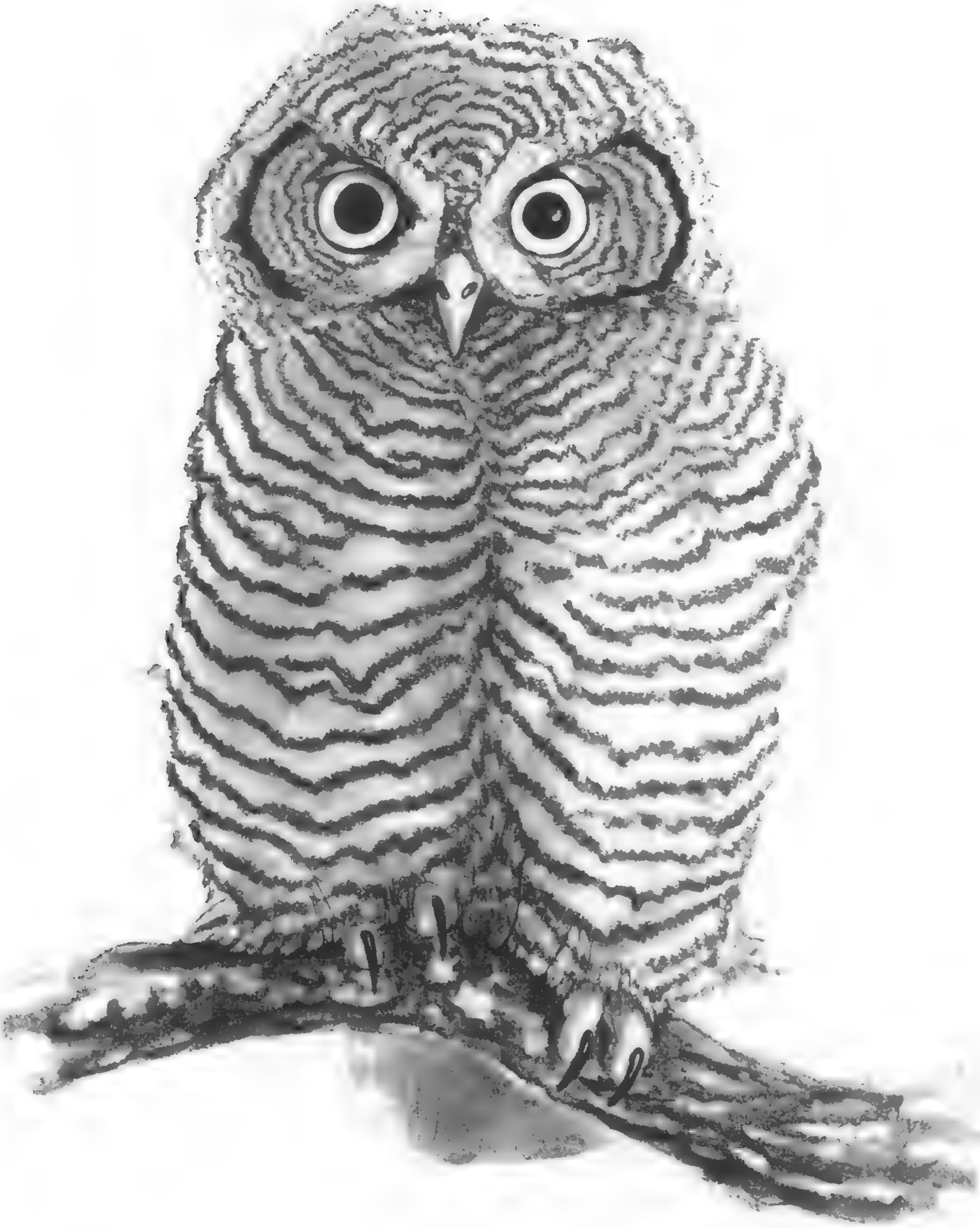

Screech Owl, *Otus asio*. Drawing by Tony Angell.

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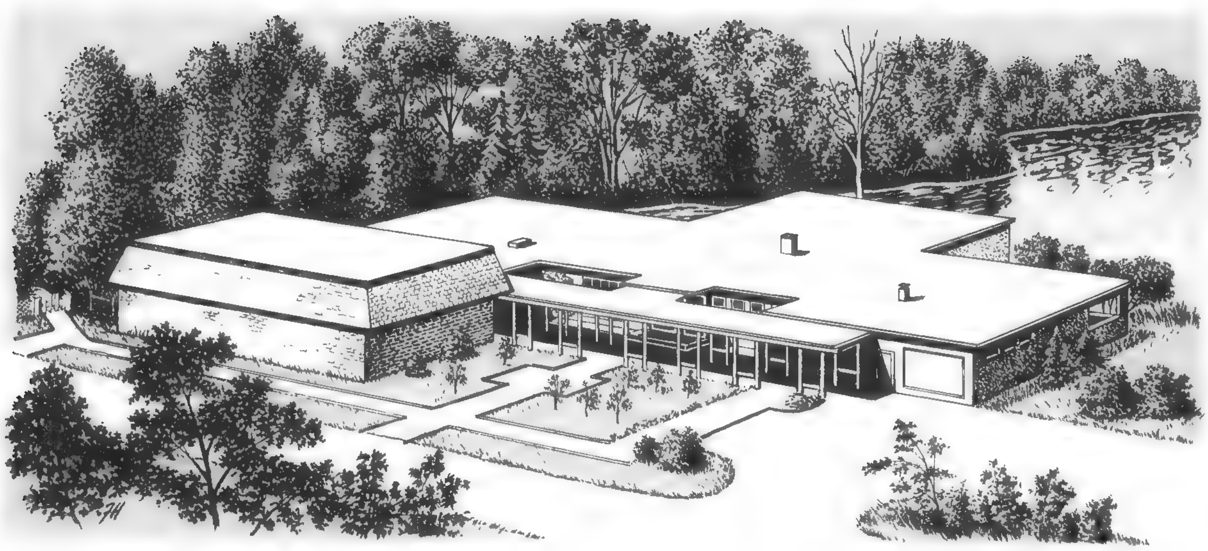

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The Cornell Laboratory of Ornithology is a center for the study and cultural appreciation of birds, with headquarters in Sapsucker Woods, three miles from the main campus of Cornell University at Ithaca, New York. The Laboratory is open almost every day of the year and visitors are welcome whenever the building is open.

A separate department within the administrative complex at Cornell University, the Laboratory is primarily concerned with scientific and educational activities.

Through the cooperation of many hundreds of bird observers in the United States and Canada, the Laboratory gathers statistical data on the nesting of all North American species and analyzes the data to determine population trends, rates of survival, and other phenomena.

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# THE LIVING BIRD

**TWELFTH ANNUAL........1973**

*Cornell Laboratory of Ornithology*

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## of Ornithology
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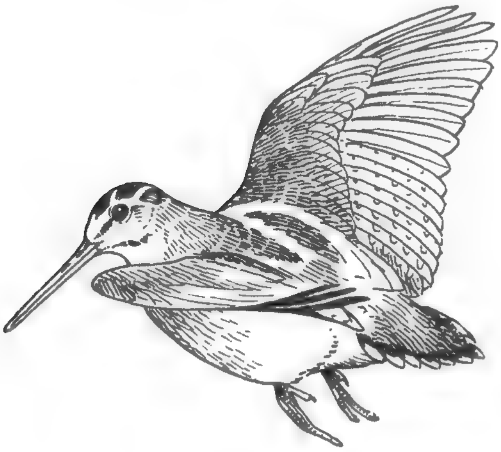

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Gannets, *Morus bassanus*. Photograph by Mary M. Tremaine.

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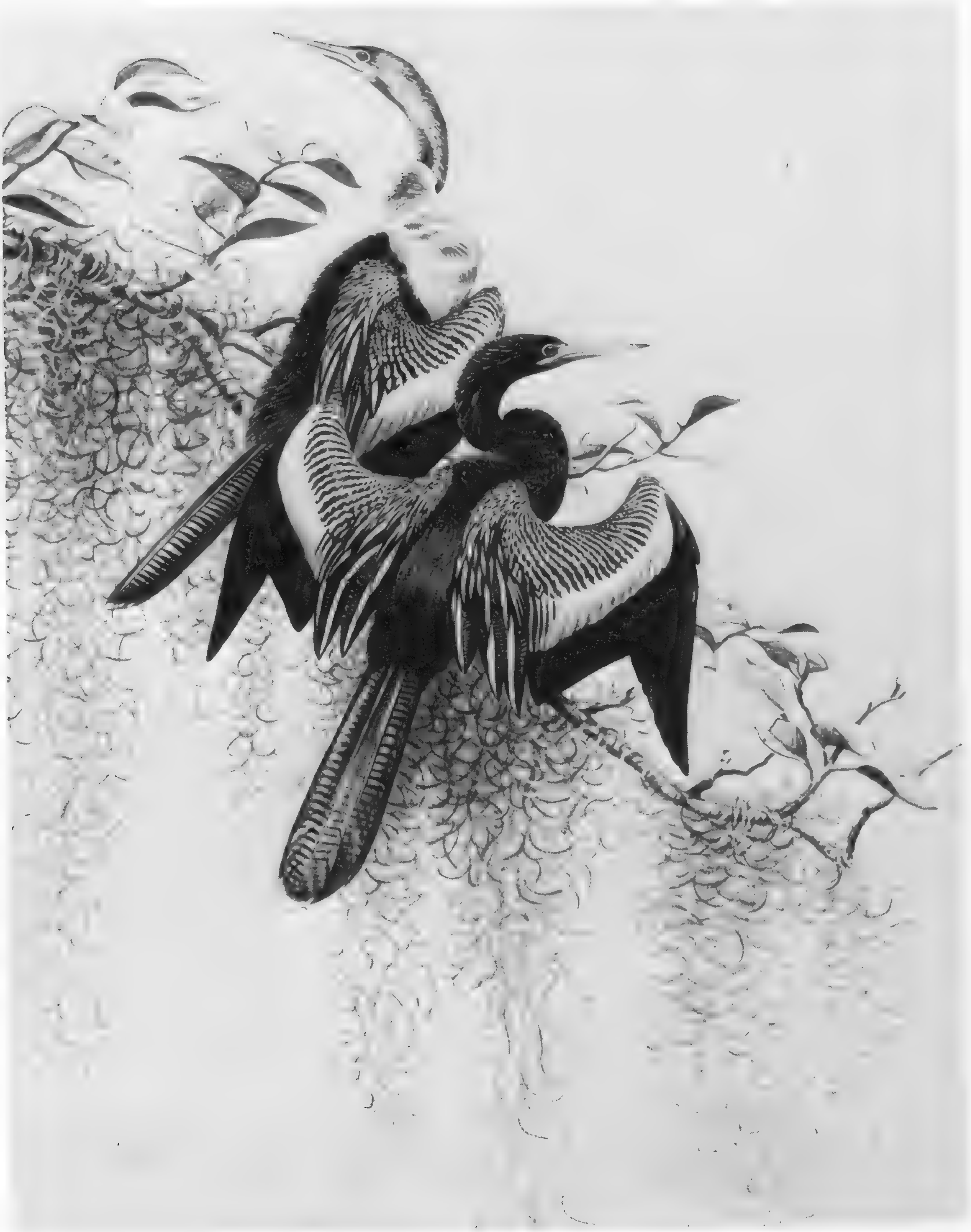

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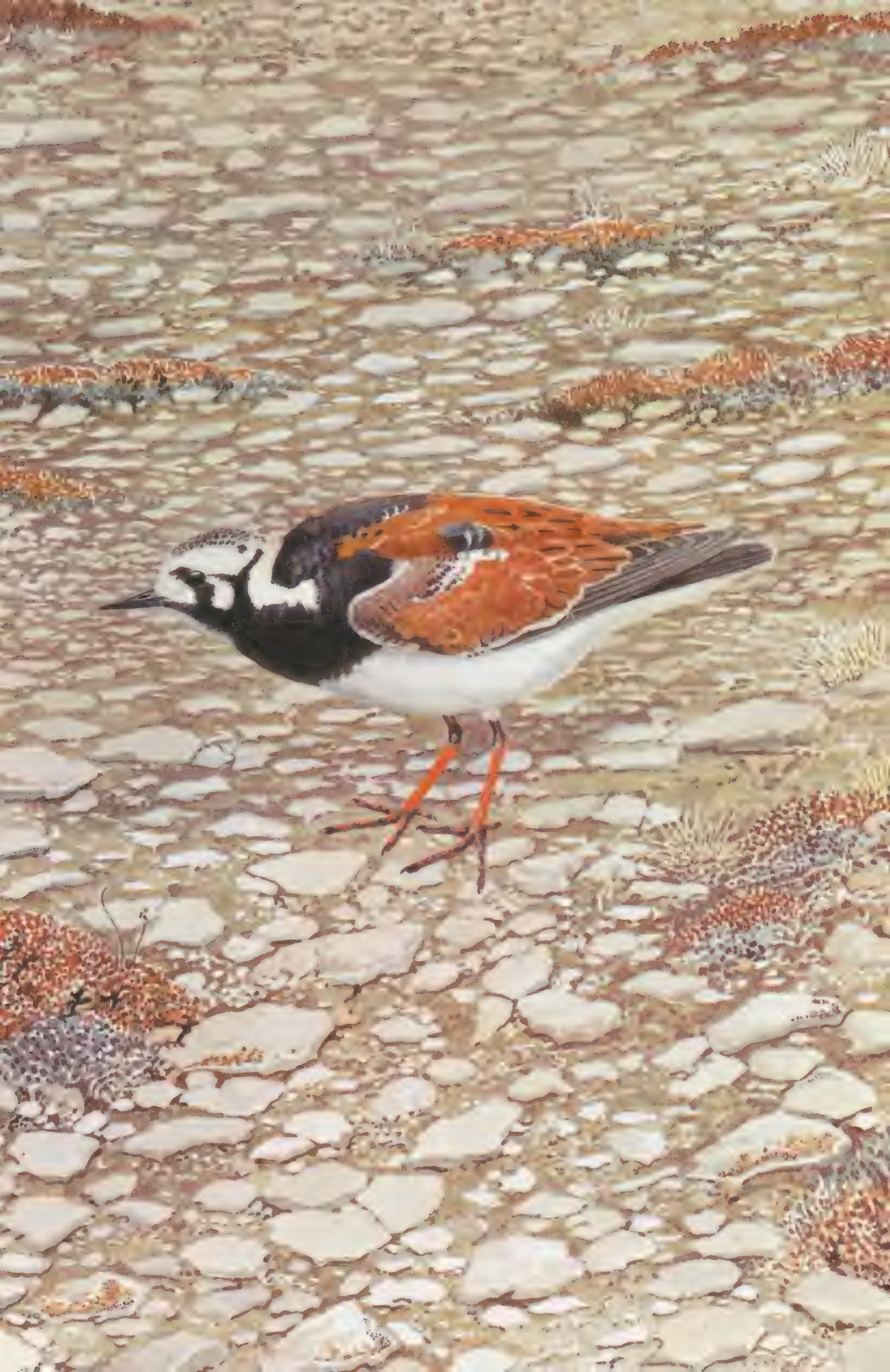

# MIGRATORY PATTERNS OF RUDDY TURNSTONES IN THE CENTRAL PACIFIC REGION[1]

MAX C. THOMPSON

This boldly patterned shorebird breeds in the boreal regions of the world and covers vast distances during migration to winter along the coasts of the United States, Central and South America to Peru and on oceanic islands, Australia, New Zealand, and South Africa.

Many details of the migratory behavior of this arctic breeder remain to be learned. Although Ruddy Turnstones (*Arenaria interpres*) have been banded in large numbers, only six recoveries were filed in the United States Banding Laboratory through 1964; all were birds banded in the eastern half of the North American continent or on islands of the Canadian Archipelago.

We knew little about the migratory routes of the Ruddy Turnstone in the Central Pacific region in 1964, when the Smithsonian Institution's Pacific Ocean Biological Survey Program (POBSP) chose this species for special study because of its abundance in the Central Pacific in winter. To obtain the maximum data, Winston Banko and J. Vincent Hoeman made a preliminary survey in Alaska in the spring of 1964, and learned that great concentrations occurred on St. Paul and St. George Islands in the Pribilof Islands during the fall migration. We decided to put our full efforts into banding turnstones on St. George Island.

## *Methods*

### Trapping

St. George Island was uniquely suited for mass banding of turnstones (See Appendix). Every year several thousand northern fur seals (*Callorhinus ursinus*) were killed and their carcasses left on two of the fields to rot (now the carcasses are removed to a dump and buried). Within hours of the kill, blowflies (*Calliphora vomitora*) laid their eggs on the carcasses, which the larvae reduced to a mass of bone within three weeks. The larvae then buried themselves in the ground around the carcass or in nearby bunches of grass. Turnstones concentrated in these areas, feeding on the larvae, making it feasible to trap them in large numbers.

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**Ruddy Turnstone, *Arenaria interpres*. Painting by George Miksch Sutton.**

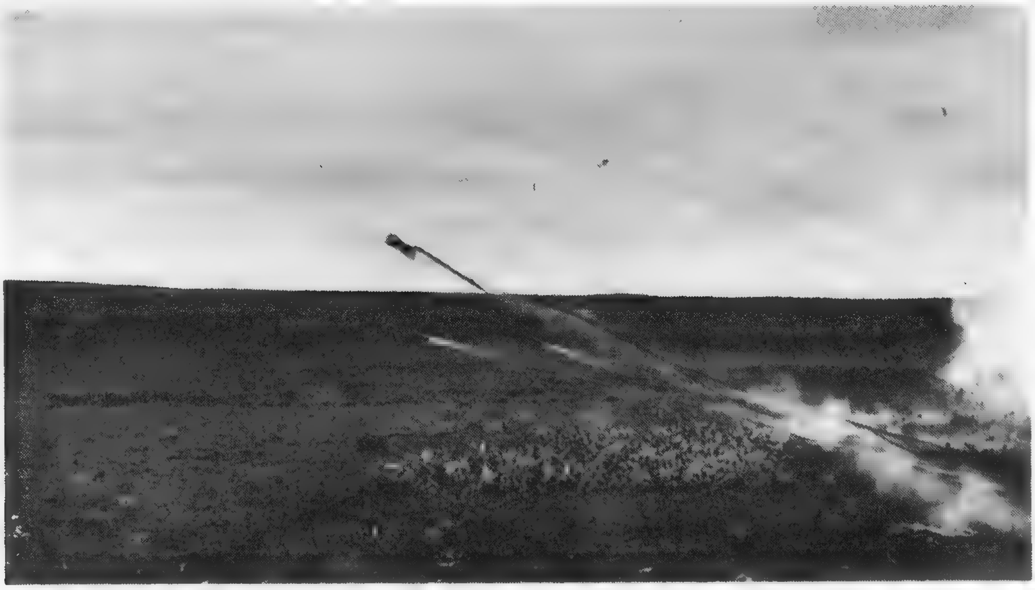


Figure 1. Rocket-net engulfing a flock of Ruddy Turnstones. Note elevation of birds. Picture taken at 1/1000th of a second.

The initial trapping attempt with Japanese mist nests in July 1964 failed due to inclement weather, high winds, and predation by the abundant Arctic fox (*Alopex lagopus*). We then decided to use a cannon net (Figures 1 and 2). In one shot, we trapped as many turnstones as we had netted during the previous three weeks. The cannons we used were fired by commercially prepared, electrically-detonated charges. Not satisfied with these cannons, we obtained a new and far superior type of rocket projectile in 1966 manufactured at that time by Central Technology Incorporated. The new rockets were extremely satisfactory.

We also changed the size of mesh on the cannon net from one and one-half inch used in 1964 to a one-inch mesh in 1965. Both nets measured 75 by 35 feet and, when projected, many turnstones were able to out-fly the hurtling net and escape. From 1966 to 1968 we used a 75 by 50-foot net with four rockets attached. Although the turnstones were able to become airborne, the net overtook them and dropped ahead of them. We have described our rocket-netting procedures more fully elsewhere (Thompson and DeLong, 1967).

The position of the net on the field was extremely important. Observations of the feeding behavior of the turnstones revealed that the area in which they fed changed daily, so we exercised care to avoid disturbing the flock upon our initial approach in the morning. Eventually we found we could set the net up the night before and, by crawling on our hands and knees (a most unpleasant job among the rotting carcasses of fur seals), we could herd the birds toward the net if they happened to change feeding areas. Initially, we hid the net with cut grass but later used nylon camouflage netting. Still later we found that by placing nets on different fields and leaving them for several hours uncamouflaged, the birds tended to ignore them. However, the Arctic fox did not ignore them, and it was infuriating, after a wait of several hours, to have hundreds of turnstones in front of a net only to find, when you tried to detonate it, that a fox had chewed the firing cord in two!

From 1965 to 1968, we placed captured birds in cages (Figure 3). We had only two cages, each with 60 compartments, and occasionally we trapped more birds than we could store. The birds were then taken to an old fox shed (Figure 4), which had been converted for our use. Fox sheds were used in the period from 1920 to 1950 to trap foxes, fatten them until their pelts were prime, and harvest them. It was not uncommon to have 300 to 400 birds in a shed waiting for banding. They were quite tame and we could band them at our leisure.

## Banding

We banded turnstones from 1964 to 1966 with United States Fish and Wildlife Service aluminum bands. These proved unsatisfactory, since wear and abrasion caused by turnstones' feeding habits rendered many illegible within one year. In 1967, we obtained

Incoloy bands from England and rebanded all returns as well as the new birds (Thompson, 1970). Bands recovered in 1972 by Ronald G. Pletnikoff on St. George Island were almost like new. The stiff Incoloy bands require special pliers to crimp them.

We banded the birds as soon as possible after capture. Many were weighed. We color-marked most of them on the white rump with high visibility red-orange paint, which was effective for about five months. In 1964, twelve of the thirteen recoveries were color-marked birds. We also used leg streamers for two years but these soon wore off.

In the cool damp climate of the Pribilof Islands, it was impossible to wait until the ground had dried before firing the net. Its weight, combined with the struggling of the birds on muddy fields, so soiled the birds that they could not fly and would have perished without corrective measures before releasing them. Wet turnstones were kept in captivity until dry. If they had mud and grease on them, they were taken to our living quarters, washed, and kept in a warm room until completely dry. This operation was completely satisfactory and no ill effects were noted.

The turnstones showed very little fear at being handled in the banding and weighing process. It was not uncommon to have turnstones sitting on our shoulders or head as we worked.

We also found that some fat birds that struggled in the nets were unable to fly after they were banded. These birds, when held overnight, usually had sufficient energy to depart.

### Weighing

During the course of the study, we weighed approximately 2,200 newly netted turnstones and 600 recaptures on a triple-beam balance to the nearest tenth of a gram. We pursued the weighing program most diligently in 1965, our goal being to try to determine the weight accumulation necessary before a turnstone reached the threshold of adequate energy reserves that would allow it to migrate over water for a long period.

We calculated the mean weight of each day's captives and plotted the daily fluctuations in mean body weight.

## *Changes in Weight*

The turnstones we weighed ranged from 85 to 195 grams. The lighter birds were usually juveniles. Extremely heavy birds probably had been on the island for some time, while the light birds were likely new arrivals. The

Figure 2. Robert L. DeLong arranging camouflage on rocket net.

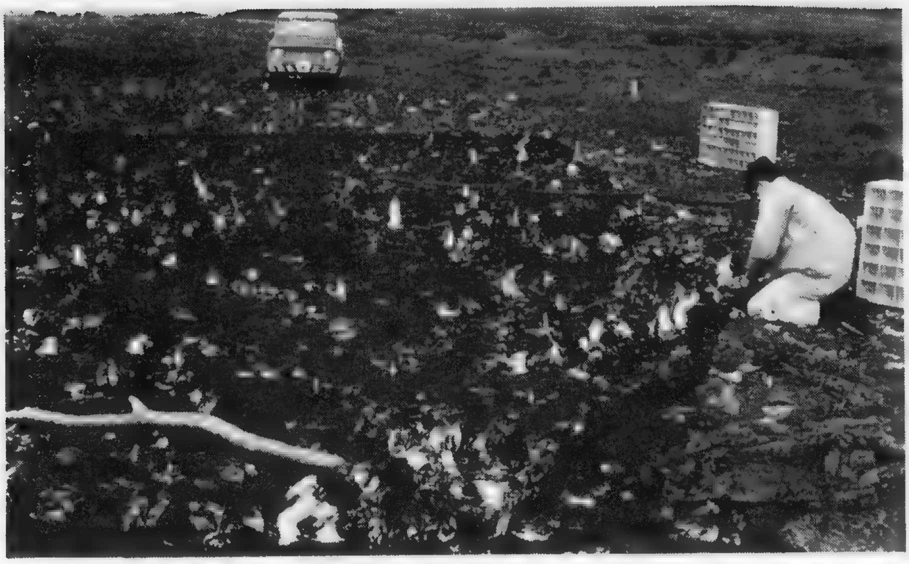


Figure 3. Robert L. DeLong removing Ruddy Turnstones from under the rocket net with 60-compartment holding cages awaiting the birds for banding.

majority of turnstones departed when they weighed about 153 gm. The turnstone recovered from French Frigate Shoals (see Fall Migration section) weighed 154.8 gm on 27 August, just prior to its departure.

We were unable to determine whether birds weighing more than 153 gm lost the excess weight before departure or retained it. The build-up of excessive fat may have been due to inclement weather that prevented southward migration and allowed the birds to store large quantities of fat from feeding on the island's abundant food supply (Figure 5). Some birds were so heavy that after struggling under the net for an hour they were unable to fly unless tossed high into the air; lighter birds departed under their own power. Palmer (1899:410) remarked that the Aleut children were able to run the turnstones down on the fields because they were so heavy with fat. Hoeman ran one down in 1964 but this appears to be exceptional; I never saw an untrapped bird that could not fly.

All birds that we recaptured were reweighed. When we processed these data, it became readily apparent that immediately after banding, birds tended to lose weight for a few days (Table 1). All birds reweighed within one day of original banding had lost weight, and more than 50 per cent of the birds weighed less up to five days after initial banding. From day six until the last weight was taken, more than 50 per cent of the birds gained weight.

I attributed the weight loss to several factors. Probably the major cause was fatigue from struggling under the net. After being banded, birds remained on the beaches and tundra, resting and using the fat supply already accumulated, instead of returning to the field to feed. We noted that some netted birds had rubbed the underneath side of the wings on the net until they oozed blood. These birds were able to fly but probably did so only when frightened. The shock of being netted and handled may also have contributed to the weight loss. The records show that the majority of the birds were not recaptured until several days after the initial banding, indicating they were reluctant or unable to come to the feeding area.

Mueller and Berger (1966) also noted decline in the weights of Swainson's Thrushes (*Hylocichla ustulata*) after they had been banded.

## *Returns in Longevity*

We banded 16,152 turnstones from 1964 through 1967 (birds banded in 1968 are not included since no study was made in 1969). The number of returns to the Pribilof Islands from 1964 to 1968 was 3,223, a return rate of 21.47 per cent (immatures banded in 1967 are not included). Of these returns, 1,464 or 75 per cent were rebanded with Incoloy bands. The rebanding figures show the extreme wear on aluminum bands by turnstones. It is interesting to note that several birds returned more than once over a four-year span: 118 were captured twice; 26 returned three years; and three birds were picked up in each of the four years subsequent to their banding. Some of these birds were also captured, recorded, and released during the spring migration in Japan. One turnstone (652-48085), banded in 1964 as an adult, returned to the banding station in 1965 and 1967 and was subsequently captured, recorded, and released by the Japanese near Tokyo in the spring of 1971. We banded this bird as an adult, and, since first year birds do not migrate north in any numbers, we can assume it was at least two years old when banded, indicating a minimum age of nine years in 1971. We hope that additional band returns in future years will provide more longevity records. Table 2 gives the number of returns for the years after the birds were banded.

## *Food and Feeding Behavior*

The feeding behavior was such an integral part of the banding operation that I will describe it. The turnstones fed primarily in the "killing fields," the areas used by the National Marine Fisheries Service for the fur seal harvest. The first seal kills were usually in early July, about the time the first turnstones arrived from the breeding grounds (turnstones do not breed in the Pribilof Islands). By the end of July, turnstones were present in high numbers and were feeding on the blowfly larvae.

In 1964, we analyzed stomach contents of birds taken in early August, and thought their diet was composed mainly of adult insects picked up on the field. Preble and McAtee (1923:80) summarized the prior analysis of stomach contents from the Pribilof Islands: "As in the case of the Pacific Golden Plover, Elliot and Hanna both assert that turnstones feed almost exclusively on maggots in the seal-killing fields during their stay on the

Figure 4. Fox shed on East Killing Field. High bluffs in the background are the highest points on the island of St. George. Note seal skeletal remains in the foreground.

TABLE 1

Per Cent of Birds Losing or Gaining Weight After Banding

| *Number of days after initial banding* | *Per cent losing weight* | *Per cent gaining weight* | *Total number weighed* |
|---|---|---|---|
| 1 | 100.0 | 0 | 7 |
| 2 | 76.9 | 23.1 | 13 |
| 3 | 55.0 | 45.0 | 20 |
| 4 | 68.2 | 31.8 | 22 |
| 5 | 75.0 | 25.0 | 24 |
| 6 | 48.7 | 51.3 | 39 |
| 7 | 47.1 | 52.9 | 17 |
| 8 | 50.0 | 50.0 | 24 |
| 9 | 48.4 | 51.6 | 31 |
| 10 | 36.7 | 63.3 | 30 |
| 11 | 42.3 | 57.7 | 26 |
| 12 | 46.4 | 53.6 | 28 |
| 13 | 26.7 | 73.3 | 30 |
| 14 | 42.9 | 57.1 | 21 |
| 15 | 27.3 | 72.7 | 22 |
| 16 | 26.3 | 73.7 | 19 |
| 17 | 26.9 | 73.1 | 26 |
| 18 | 5.9 | 94.1 | 17 |
| 19 | 23.8 | 76.2 | 21 |
| 20 | 14.3 | 85.7 | 14 |

Pribilof Islands. The 12 well-filled stomachs of the birds from the islands do not bear out such far-reaching statements, but these larvae did compose most of the contents of one stomach."

Of the 30 stomachs examined in 1965, nine contained insects other than blowflies, two had stones, and 19 carried blowfly larvae. The samples, taken over a period of two months, tend to show why the disparity in observations arose. The nine samples with insects other than blowflies were taken prior to 16 August, and samples taken after 16 August contained blowfly larvae. Turnstones apparently fed primarily on other insects until the blowfly larvae had grown, left the carcasses, and embedded themselves in the ground or clumps of grass. Maggots migrated from the carcasses at night, and on several occasions just prior to sunrise, the ground looked snow-covered because of the density of departing maggots. We never saw turnstones take maggots directly from the carcass.

Others have observed turnstones eating maggots, but with adverse effects. On Cape Cod, Austin and Austin, Jr. (1931) found dead turnstones and other shorebirds in the vicinity of some rotting carcasses; other birds,

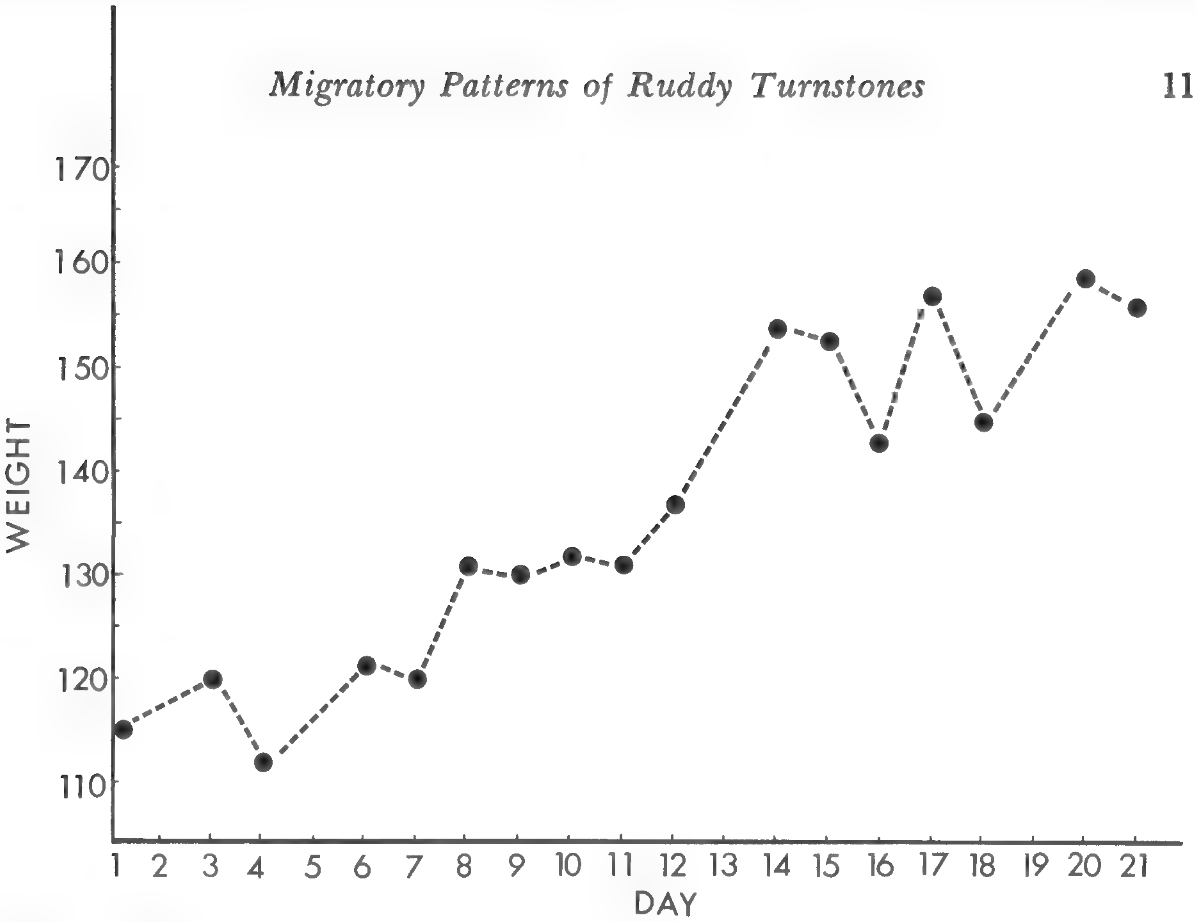


Figure 5. Daily fluctuations in the mean body weight of Ruddy Turnstones on St. George Island in August.

alive but sick, evidently were suffering from botulism. The sick birds were given fresh water and food and eventually recovered (see Cooch [1964] for a discussion of botulism and fresh water). We never observed a case of botulism in the many thousands of Ruddy Turnstones on the Pribilof Islands.

Other kinds of food also were noted in the diets of the turnstones, the most common being a small periwinkle found in abundance on the rocks at low tide. Additional data from the Central Pacific showed that crustaceans are probably a major source of food during the winter months (POBSP records). Of the 42 stomachs examined from the Hawaiian and Phoenix Islands, 21 contained remains of crustaceans, primarily small sand crabs. Another 18 contained insect remains. Some stomachs contained both insect parts and crustacea. Four stomachs contained some plant material. Crossin and Huber (1970) found turnstones preying on the eggs of the Sooty Tern (*Sterna fuscata*).

The method of feeding by turnstones on St. George varied with the time of year. Before the maggots emerged from the carcasses and burrowed into the ground, the birds went about the fields flipping over the seal bones left from previous years, the largest objects turned being scapulas about six inches square. They took small insects from under the bones with a swift jab of the bill. After the maggots burrowed into the ground, the turnstones turned the soil until certain areas of the field looked as though they had been plowed. The birds put their bills into the ground and began rooting by alternately flipping the bill up, or sideways, then burying it again. They rooted quite vigorously and often dug quite deeply, being almost hidden from view on occasions.

We do not know whether turnstones have used the killing fields on St. George Island since 1968 when the National Marine Fisheries Service sold

TABLE 2

Banding and Recoveries of Ruddy Turnstones

| | | *Recoveries** | | | | |
|---|---|---|---|---|---|---|
| | *Banded* | *1965* | *1966* | *1967* | *1968* | *Totals* |
| 1964 | | | | | | |
| Adults | 844 | 125 | 122 | 87 | 46 | 380 |
| Immatures | 1,218 | 1 | 111 | 83 | 29 | 224 |
| Foreign recoveries | | — | — | — | — | 20 |
| 1965 | | | | | | |
| Adults | 3,304 | — | 547 | 393 | 271 | 1,219 |
| Immatures | 123 | — | — | 6 | 2 | 8 |
| Foreign recoveries | | — | — | — | — | 49 |
| 1966 | | | | | | |
| Adults | 4,336 | — | — | 594 | 498 | 1,092 |
| Immatures | 3,118 | — | — | 2 | 69 | 71 |
| Foreign recoveries | | — | — | — | — | 65 |
| 1967 | | | | | | |
| Adults | 2,063 | — | — | — | 207 | 207 |
| Immatures | 1,146 | — | — | — | 3 | 3 |
| Foreign recoveries | | — | — | — | — | 38 |
| 1968 | | | | | | |
| Adults | 1,643 | — | — | — | — | — |
| Immatures | 706 | — | — | — | — | — |
| Foreign recoveries | | — | — | — | — | 26 |

*All but "foreign recoveries" were on St. George Island, Pribilof Islands, Alaska.

the carcasses to the Japanese to be processed (returning bits of the carcasses to the field for our study). The killing of fur seals on St. George was suspended in 1973. On St. Paul Island, the carcasses have been processed for mink food for a number of years and there are now no large concentrations of turnstones. Until the removal of carcasses from St. Paul, the flocks of turnstones were apparently as large as those on St. George. Beginning in 1972, the carcasses on St. George Island were removed to the dump and turnstones no longer gather in large numbers on the killing fields (Ronald G. Pletnikoff, pers. commun.).

Turnstones probably have utilized the Pribilof Islands as feeding stations for thousands of years. Enormous numbers of seals inhabited the islands prior to the arrival of man in 1786. Natural mortality must have ensured the presence of many carcasses on the beaches where, although still present, their numbers are not significant in providing a major source of food for the turnstones.

The birds were extremely territorial while feeding, although the territories were not over a foot in diameter. Individuals clashed sharply when one bird got too close to another. When we had up to 400 birds indoors at one time, certain individuals set up and defended territories.

Vocalizations accompanying feeding were important, as was the size of the feeding flock. The flock wheeled over the field but normally did not land as a flock until at least ten birds were on the ground. The first few birds on the ground were particularly nervous and flew off at the slightest provocation. The "all clear" for the entire flock to land appeared to be a gabbling call. Birds continued this gabbling sound while feeding and ceased when danger appeared. When the gabbling stopped, all birds stopped feeding and began to survey the area for the source of danger. The birds we had in captivity on St. George made this gabbling sound continually, and it seemed to be related to the birds' territories. When we appeared, one bird gave a sharp whistle and the gabbling stopped immediately; it commenced again as soon as we became motionless. When we moved, the sharp whistle once more caused the gabbling to stop. I feel certain this alarm note alerted the birds to a potential source of danger on the field but, with several thousand birds gabbling at once, it was impossible to distinguish it.

## *Fall Migration*

The migratory path of the Ruddy Turnstones that pass through the Pribilof Islands can now be delineated with fair certainty. The birds breed in Siberia and on St. Lawrence Island. In July they leave the breeding grounds and pass southward to the Pribilof Islands. Most birds probably remain on the Pribilofs for two to three weeks before moving on to the wintering grounds in the Central and Southwest Pacific Ocean region.

The first birds arrived at St. George Island in early July (11 July 1965, 12 July 1966, 9 July 1967, 10 July 1968) and reached their peak numbers about 15 August when flocks of 10,000 birds were not uncommon on the killing fields.

The first large migration southward from the Pribilof Islands began around 15 August and continued in lesser numbers well into October. However, the main mass of birds departed prior to 1 September.

During the fall, turnstones show a definite differential migration between adults and young of the year. Adults appeared first. The earliest young birds arrived during the first week of August, gradually increasing in numbers until, by the third week of August, they were the dominant age group. However, in 1965 there was apparently little breeding success. That year we banded 3,304 adults and only 123 young, compared to 4,336 adults and 3,338 young in 1966. Francis H. Fay (pers. commun.) corroborated the low production in 1965 with his observations of the breeding birds on St. Lawrence Island, where the summer was cold and wet and nesting success greatly reduced.

The cloud cover hovers over the Bering Sea almost constantly in summer. The first break in the cloud cover during August started a mass exodus of turnstones from the Pribilof feeding grounds. During the five years we banded on St. George Island, this break occurred around 16–17 August and numbers departing declined from then on. While a break in the normal cloud cover appeared necessary for departure from the Pribilofs, no such break in cloud cover is necessary for arrival. The build-up in turnstone populations on the Pribilofs takes place during heavy cloud cover; since the cloud layer is not high, the birds would still be able to navigate by the stars and sun, finding the islands and coming down through the fog to land. On one clear day we noted turnstones arriving at St. George Island from the north between 10:00 and 11:00 hours. We first heard them, then saw them flying quite high. We calculated that by flying 30 to 40 miles per hour, and having left land at about 18:00 hours the previous day, their departure point would have been somewhere around Cape Navarin, Siberia. Recoveries from Siberia lend credence to this conjecture (see Weather and Fall Migration for further notes).

When turnstones depart from the Pribilof Islands on their southward migration, there is no land, except the Aleutian Islands, for them to rest on before reaching the northwestern Hawaiian Islands. The closest island to St. George is Kure Atoll, 1,991 statute miles southwest. Indications are that the Aleutian Islands are little used for rest stops. Color-marked turnstones have been sighted, but in no great numbers, at Umnak, which lies almost directly south of St. George. Banded birds also have been collected at Amchitka Island, but no large numbers are known to use the island during fall migration. Murie's (1959:135–136) observations in the Aleutians tend to support this observation. Robert Jones (pers. commun.) reported large numbers of turnstones at Cold Bay on the tip of the Alaska Peninsula, but never saw a color-marked bird. This suggests that the birds found on the mainland are most probably birds breeding on mainland Alaska.

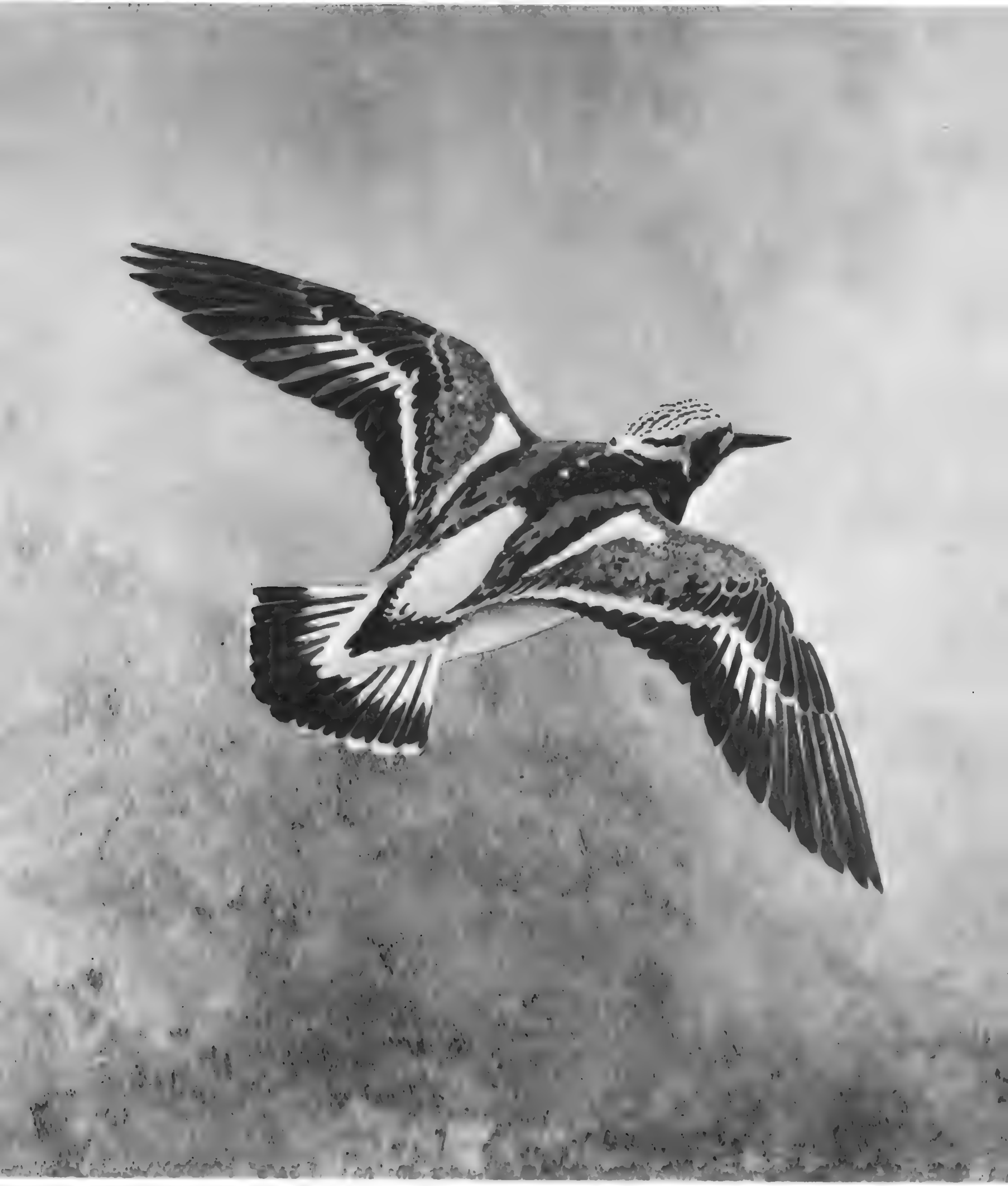
Turnstones can land on the water momentarily and get off again. We have seen them swimming across shallow ponds on St. George Island, and MacMillan (1918:408–409) saw a flock alight on salt water between two islands. His observation is the only one I can find indicating that they do so even occasionally.

The Pribilof turnstones probably fly nonstop to the Hawaiian Islands or the Marshall Islands. One remarkable record is that of number 712-06593. We banded this bird on St. George Island on 23 August 1965. It was recaptured on 27 August and collected 31 August on French Frigate Shoals in the Northwestern Hawaiian Islands, a distance of 2,272 miles. If the bird departed on 27 August at 18:00 hours, it would have had to cover the distance in three-and-one-half days, or 649 miles per day. Flying night and day for 88 hours, this turnstone flew 27 miles per hour. We have clocked Ruddy Turnstones at a ground speed of 40 mph. If the turnstone could have sustained this higher speed, it could have made French Frigate Shoals in 55 hours instead of our calculated 88. This turnstone weighed 174.0 gm when we banded it on 23 August. On 27 August, when recaptured, it weighed 154.8 gm, a loss of 19.2 gm in four days. Unfortunately, the bird could not be weighed when collected on French Frigate Shoals, because the station balance was broken.

This turnstone was collected under unusual circumstances. The POBSP personnel then on French Frigate Shoals were just boarding a Coast Guard aircraft to return to Honolulu when a flock of turnstones, including one color-marked bird, flew past the plane. Since the collecting equipment had been packed and was unavailable, an M-1 rifle was borrowed from Coast Guard Loran Station personnel. Three shots, none of which hit the bird, were fired; the third shot knocked a piece of asphalt out of the runway and killed the bird.

Thomson (1936) lists the record of a turnstone banded at the Heligoland Island lighthouse and released at 11:00. The bird was shot 25 hours later at Quineville on the north coast of France. This was a direct-line distance of about 510 miles for an average of 480 miles per day.

Table 3 gives some of the more interesting fall recoveries. Additional locality records can be found in Appendix I.

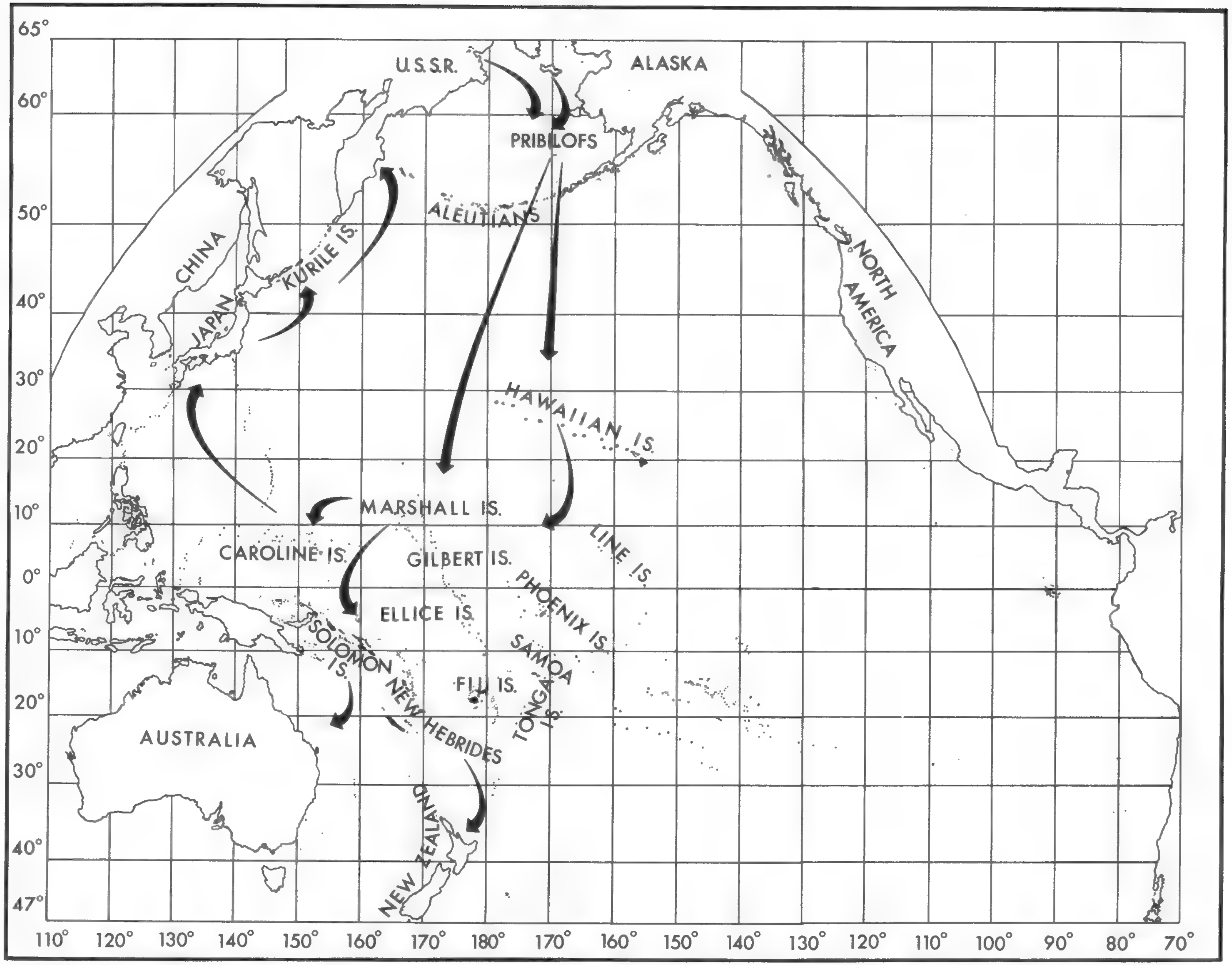


Ruddy Turnstone, *Arenaria interpres*. Painting by George Miksch Sutton.

## TABLE 3

### Selected Fall Recovery Records of Birds Banded at St. George Island, Pribilof Islands

| *Locality* | *Date banded* | *Date recovered* | *Miles travelled* | *Miles per day (statute)* |
|---|---|---|---|---|
| Hawaiian Islands | | | | |
| Kure | 5 Aug. 1966 | 28 Aug. 1966 | 1,991 | 87 |
| Kure | 6 Aug. 1966 | 2 Sept. 1966 | —— | 74 |
| Kure | 11 Aug. 1966 | 8 Sept. 1966 | —— | 71 |
| Kure | 10 Aug. 1966 | 9 Sept. 1966 | —— | 66 |
| Pearl and Hermes Reef | 18 Aug. 1967 | 28 Aug. 1967 | 2,001 | 200 |
| Lisianski | 8 Aug. 1967 | 4 Sept. 1967 | 2,119 | 79 |
| Laysan | 3 Aug. 1967 | 6 Sept. 1967 | 2,140 | 63 |
| Laysan | 9 Aug. 1967 | 6 Sept. 1967 | —— | 76 |
| Laysan | 17 Aug. 1967 | 6 Sept. 1967 | —— | 107 |
| French Frigate Shoals | 29 July 1966 | 19 Aug. 1966 | 2,272 | 108 |
| French Frigate Shoals | 11 Aug. 1966 | 26 Aug. 1966 | —— | 152 |
| French Frigate Shoals | 11 Aug. 1966 | 29 Aug. 1966 | —— | 126 |
| French Frigate Shoals | 27 Aug. 1965 | 31 Aug. 1965 | —— | 649 |
| French Frigate Shoals | 1 Aug. 1965 | 2 Sept. 1965 | —— | 71 |
| French Frigate Shoals | 12 Aug. 1966 | 12 Sept. 1966 | —— | 73 |
| French Frigate Shoals | 16 Aug. 1966 | 16 Sept. 1966 | —— | 73 |
| French Frigate Shoals | 18 Aug. 1966 | 14 Sept. 1966 | —— | 84 |
| Howland Island | 12 Aug. 1966 | 20 Sept. 1966 | 3,869 | 99 |
| Howland Island | 25 Aug. 1966 | 20 Sept. 1966 | —— | 149 |
| Baker Island | 25 Aug. 1966 | 18 Sept. 1966 | 3,908 | 163 |
| Baker Island | 18 Aug. 1966 | 14 Oct. 1966 | —— | 69 |
| Phoenix Islands | | | | |
| McKean | 20 Aug. 1965 | 23 Sept. 1965 | 4,160 | 122 |
| Hull | 7 Aug. 1966 | 7 Oct. 1966 | 4,215 | 136 |
| Marshall Islands | | | | |
| Taka Atoll | 24 Aug. 1968 | 20 Oct. 1968 | 3,339 | 56 |
| Eniwetok | 20 Aug. 1968 | 12 Sept. 1968 | 3,455 | 150 |
| Eniwetok | 5 Aug. 1968 | 14 Sept. 1968 | —— | 86 |
| Mejit | 1964 15 Sept. | 22 Aug. 1964 | 3,361 | 160 |
| Arno | 4 Sept. 1966 | 25 Sept. 1966 | 3,564 | 170 |
| Ailinglapalap | 2 Sept. 1964 | 18 Sept. 1964 | 3,598 | 225 |
| Majuro | 14 Aug. 1966 | 9 Sept. 1966 | —— | 138 |
| Majuro | 26 Aug. 1966 | 19 Sept. 1966 | —— | 150 |
| Majuro | 21 Aug. 1964 | 26 Sept. 1964 | —— | 100 |
| Majuro | 23 Aug. 1966 | 28 Sept. 1966 | —— | 100 |
| Majuro | 4 Sept. 1966 | 28 Sept. 1966 | —— | 150 |
| Mili | 13 Aug. 1967 | 4 Sept. 1967 | 3,631 | 165 |
| Johnston Atoll | 19 Aug. 1966 | 29 Aug. 1966 | 2,749 | 275 |
| Ellice Islands | | | | |
| Nanumea | 18 Aug. 1966 | 1 Sept. 1966 | 4,370 | 316 |
| Santa Cruz Islands | | | | |
| Utupua | 19 Aug. 1968 | — Aug. 1968 | 4,882 | ? |


65°
60°
50°
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130°
120°
110°
100°
90°
80°
70°
U.S.S.R.
ALASKA
PRIBILOFS
ALEUTIANS
CHINA
JAPAN
KURILE IS.
NORTH AMERICA
HAWAIIAN IS.
MARSHALL IS.
CAROLINE IS.
GILBERT IS.
LINE IS.
PHOENIX IS.
ELLICE IS.
SAMOA
SOLOMON IS.
FIJI IS.
TONGA IS.
NEW HEBRIDES
AUSTRALIA
NEW ZEALAND

Figure 6. The circular migration route of the Ruddy Turnstone in the Pacific Ocean region.

## *Wintering Grounds*

Turnstones, which breed in eastern Siberia and on St. Lawrence Island, Alaska, and pass southward through the Pribilof Islands, winter in the southwest Pacific Islands. As Figure 6 and Appendix I show, the apparent major wintering area lies in the Marshall, Gilbert, and Ellice Islands with lesser numbers occurring in the Phoenix, Fiji, and Solomon Islands. Observations of our color-marked turnstones have been made on North Island, New Zealand, as well as Bowen and Sydney, Australia. The two sightings at Sydney are at the greatest distance, 6,663 miles, from St. George Island.

More birds were recovered from the Marshall Islands than elsewhere, the first birds arriving in early September and stragglers continuing into November. Since our birds were color-marked, their chances of being noticed during the early part of September were better than later in the winter when the paint faded. Feathers from early January returns showed very little color remaining. This may be a factor in the skewed recovery record curve that showed more recoveries in early winter than during mid- and late winter.

Another factor affecting sightings of wintering birds is that some island groups have a dense human population, while others have either a sparse population or are uninhabited. The POBSP distributed flyers in the Marshall Islands and other parts of the Pacific to alert people to this project. Radio broadcasts also were made in several island groups.

Forty-two per cent of the 119 fall and winter recoveries were in the Marshall Islands, several of which are well-populated, and only 26 per cent were in the almost unpopulated northwestern Hawaiian Islands; all the recoveries from the latter are from September and March or April when biologists visited the islands. The POBSP made several winter visits to the northwestern Hawaiian Island group and found that the number of turnstones is small in winter.

The Gilbert and Ellice Islands, although well-populated and near the Marshalls, produced only seven per cent of the total fall and winter recoveries. We may assume with some confidence that the Marshall Islands are the center of distribution for migrating turnstones from the Pribilof Islands.

POBSP records of birds banded in the Phoenix and northwestern Hawaiian Islands prove that some individuals return to the same island in successive winters. Several turnstones were retaken the following winter on the island on which they had been banded. POBSP records also indicate some inter-island movement during the winter.

## *Spring Migration*

Spring migration is not as well defined as the fall movement, and is more difficult to explain. We originally believed that turnstones migrated directly northward from the wintering grounds, but this now seems only partially true. Ruddy Turnstones occur in the Pribilofs in small numbers in spring, and some birds banded there in the fall were retaken the following spring on St. George. In contrast, however, very large numbers move through the Commander Islands in the western Bering Sea (Johanson, 1961:50).

Thirty-nine of our banded turnstones were recovered during the spring migration in Japan and the USSR. Significantly, all those recoveries were of birds at least one and one-half years old. This evidence, and returns from St. George, indicate that immatures do not return to the north in significant numbers during the first year of life.

We recovered the following numbers of immatures on St. George during the first year after banding: 1965, 1; 1966, 0; 1968, 3. This is probably insignificant in the total picture (6 out of 6,311 immatures banded) and, due to the number of birds being handled in a short period of time, could even represent incorrectly read band numbers.

If the bands were read correctly, then some immatures do migrate north in the spring. Palmer (1967:258) states that "yearlings migrate, but [the] majority of them stop short of reaching breeding range; even those that go all the way remain in groups through summer." If immatures migrate northward, it must be to a very limited extent, as neither the Japanese nor the Russian workers have ever taken one of our first-year birds. Specimens taken during the summer in the central Pacific islands were a mixture of immatures and adults, indicating that immatures for the most part remain on the wintering grounds.

We do not know the migration route from the Southwest Pacific to Japan; but turnstones probably make the flight nonstop, since no spring records exist from islands lying in the migration path (Guam and the Marianas, both with human populations). The greatest known concentration of Pribilof-banded birds in Japan lies east of Tokyo (Figure 7) during the first eight days of May (extremes of 27 April to 28 May). The recovery

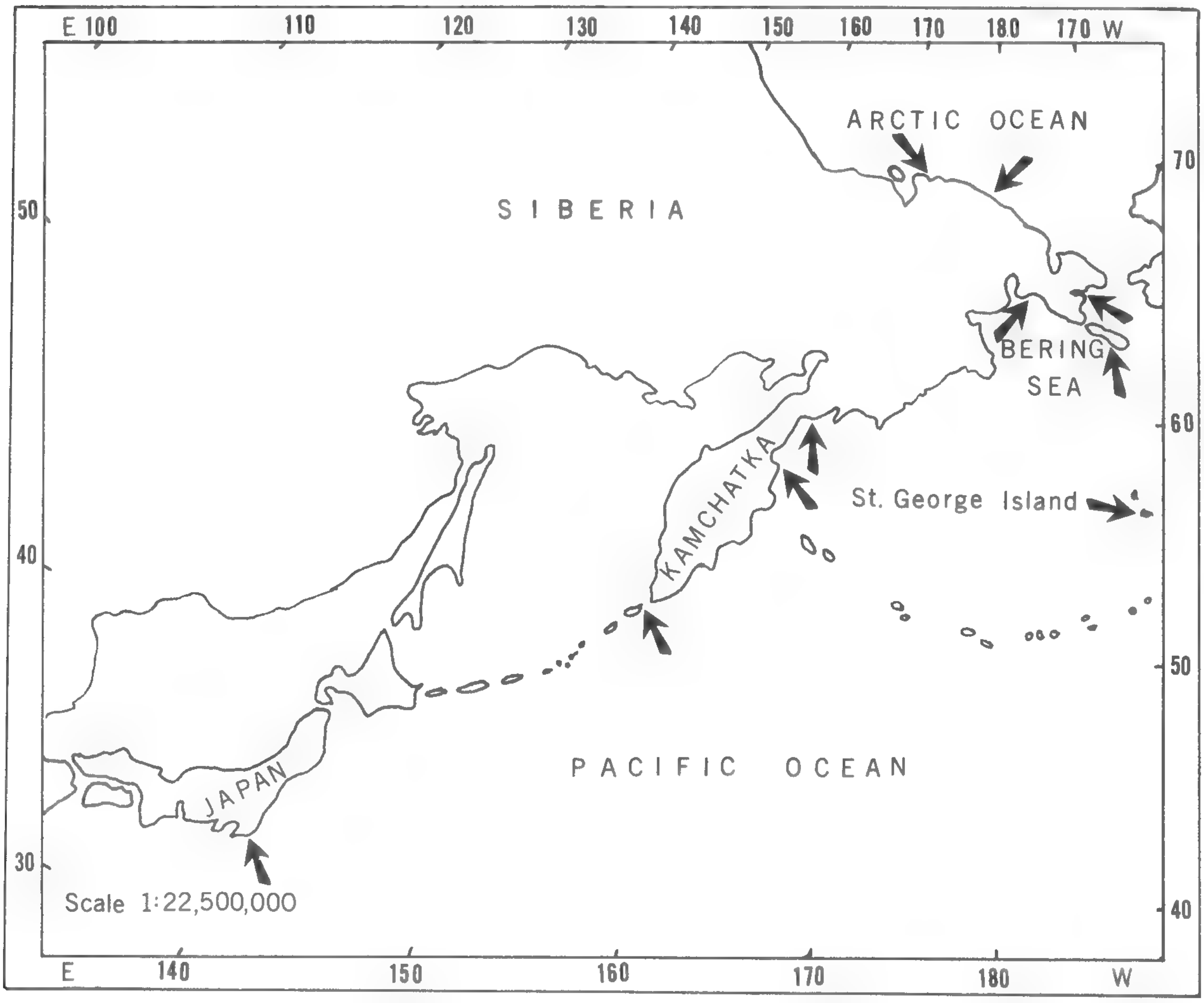

Figure 7. Spring migration route and breeding areas of the Ruddy Turnstone. Areas from which turnstones have been recovered are noted by arrow.

records from the coast of the USSR show turnstones arriving on the breeding grounds around 25 May (extremes of 30 April to 5 June). Late June recoveries are presumably from the breeding grounds. Turnstones disperse from the breeding grounds to the northern coast of Siberia (Mys Schmidt, pers. commun.) and to St. Lawrence Island, Alaska. The breeding record from St. Lawrence Island is a sighting of a banded adult male with young (later collected) by personnel from the University of British Columbia. Subsequently, two more banded turnstones were collected in June and July on St. Lawrence.

The above data suggest that the migration route is circular, southward in the fall through the central Pacific and northward in the spring through the western Pacific. However, observations of large flocks of turnstones on Laysan and Lisianski Islands by the POBSP during May and June also suggest that there may be an undefined alternate route. Only small numbers remain on these islands during the summer. A large spring banding scheme on these two islands is needed to determine the direction of their spring migratory route.

## *Weather and Fall Migration*

In 1965, we attempted to correlate weather with migration. Since St. George has no weather station, I used weather data from the United States Weather Bureau Station on St. Paul Island, 40 miles to the northwest.

We noted an increase in the turnstone population on St. George on 11 August and numbers continued to increase through 15 August. The weather at St. Paul on 11 August was overcast with winds out of the south-southwest (210°). A high-pressure cell over northern Siberia contained northerly winds capable of starting a strong southward migration in eastern Siberia. The high-pressure zone broke down 12 August, and was replaced by a low-pressure cell just north of the Bering Strait. This low still maintained a northerly flow over eastern Siberia, while high pressure south of St. George was causing southerly winds (180°). On 13 August the weather map looked very much like 12 August, but by the 14th a new low had formed over Siberia and another southwest of St. George. As these lows moved eastward, the wind at St. Paul Island began to swing to the north, but the cloud cover remained intact. On 15 August a different weather pattern appeared; winds were from the north and the clouds broke up at about 19:00 hours, allowing birds to climb up through scattered clouds and move southward. On 16 August, the population of turnstones had dropped from an estimated 10,000 birds to 1,200.

We noted another large influx of birds on 20 August. This migration probably was stimulated by a low over northern Siberia on 19 August.

The final decline in the population began on 21 August when the skies partially cleared at 22:00. It remained partly clear every night for a week, except on 24 and 26 August. By 31 August the population had declined to an estimated 1,000 birds, and by 11 September to 30 birds.

We noted similar declines with partially clearing skies in August of 1966 and 1967, but there did not seem to be an abrupt population decline in 1968. Clearing skies in August, 1965 through 1967, occurred near the middle of the month. The fact that we recorded no pronounced departure in 1968 might be attributed to cloudy skies remaining until 20 August.

We can look at a Pilot Chart of the North Pacific for the months of August to give us some idea of the average weather after the turnstones leave St. George Island. A 1968 chart shows that in August a turnstone can expect little help from the prevailing winds until it reaches the region of the northeast trades at about 30° N Lat. In fact, head winds from the southwest and south would hinder the flight. The northeast trades provide a tail wind from 30° N Lat. until about 5° N Lat., where the southeast trades prevail. To conserve energy, the line of least resistance for migrating turnstones would be southwesterly. This direction of flight seems to be supported by a complete lack of turnstone recoveries in the Line Islands, which lie directly south of the Hawaiian Islands. Turnstones occur there only in small numbers. Although the southeast trades range north to 5° N Lat. in August, the areas around the Phoenix Islands and the Solomons receive their winds from a more westerly direction, giving some head winds to the southwesterly movement (August 1968, Pilot Chart North Pacific Ocean).

Clearly, additional studies of the Bering Sea migration routes are needed. Due to the perpetual clouds over the area, radar would provide the most feasible method of tracking migrants.

## *Summary*

During the summers of 1964 to 1968, 16,152 Ruddy Turnstones (*Arenaria interpres*) were banded on St. George Island in the Pribilof Islands, Alaska. The birds were trapped with cannon nets and banded with aluminum and Incoloy bands.

The fall migration arrives on St. George Island the second week in July and continues into September. The adults arrive first with the young peaking in mid-August. Turnstones arrive on St. George in dense cloud cover but depart only when breaks in the overcast occur. The southward migration to the Central Pacific may be rapid; one turnstone averaged 649 miles per day in its flight from St. George to the French Frigate Shoals.

In 1965 the weights of captured turnstones varied from 85 to 195 grams, and averaged 153 gm upon departure. Weight losses were noted after banding.

The Ruddy Turnstones that breed in the northern Pacific and Siberia winter in the Central and South Pacific from the Hawaiian Islands to Australia, the main concentration being in the Marshall Islands.

Spring migration is not well defined but the majority of the recoveries come from Japan and the USSR in May. A circular migration route is indicated — a southward movement through the Central Pacific in fall and a northward migration in the Western Pacific in spring through Japan and into Siberia and St. Lawrence Island, Alaska, to breed.

Recaptures at the original banding site numbered 3,223, a return rate of 21.47 per cent. One adult recovered by the Japanese, released and returned to the banding station on St. George Island, was estimated to be nine years old.

The turnstones on St. George fed mainly on a variety of insects and crustaceans until mid-August when blowfly larvae (*Calliphora vomitora*) made up the main diet. The diet on the wintering grounds was mainly crustaceans.

## *Acknowledgments*

The Smithsonian Institution's Pacific Ocean Biological Survey Program funded the study from 1964 to 1966, and the National Science Foundation from 1967 to 1968 under grant number GB-6220 to Southwestern College.

Jane P. Church, Robert L. DeLong, Charles A. and Janice Ely, the late J. Vincent Hoeman, N. Joseph Kunkel, Daniel Odell, and Frank H. Smith, Jr. assisted in various years with banding operations in the Pribilof Islands. The National Marine Fisheries provided the logistics, with notable assistance from Howard Baltzo and Roy Hurd. The United States Fish and Wildlife Service and the Alaska Department of Fish and Game provided collecting permits.

I wish particularly to thank Philip S. Humphrey for his encouragement during the project, Jane P. Church and Charles A. Ely for patiently reading several drafts of the manuscript, and Dr. George M. Sutton for generously contributing his paintings of the Ruddy Turnstone for this article.

# APPENDIX

## A Listing of Localities from which Ruddy Turnstones have been Recovered and the Number Recovered at each Locality (in parentheses)

*Alaska*

St. Paul Island (2), Koozata Lagoon, St. Lawrence Island (1), Gambell (2), Amchitka Island (2)

*Hawaiian Islands*

Kure Atoll (4), Pearl and Hermes Reef (3), Midway Atoll (1), French Frigate Shoals (8), Laysan Island (5), Lisianski Island (5), Kanaluu, Hawaii (1), Johnston Atoll (4).

*Phoenix Islands*

Howland Island (2), Baker Island (2), McKean Island (1), Birnie Island (1)

*Santa Cruz Islands*

Vanikoro (2), Tikopia (1), Utupua (1)

*Solomon Islands*

Nagotana (1), Sikaiana (3), Mortlock (2)

*Banks Islands*

Star (1)

*Tonga Islands*

Tonga (1), Nukualofa (1), Niuatoputapu (2), Haapai (1)

*Fiji Islands*

Nawi (1), Tavua Bay (1)

*New Hebrides Islands*

Isles of Vate (1)

*New Caledonia*

Touho (1), "New Caledonia" (1), Isles of Pine (1)

*Ellice Islands*

Nukulaelae (1), Vaitupa (1), Nanumea (1)

*Gilbert Islands*

Abemama (1), Tarawa (2), Makin (1)

*Marshall Islands*

Jaluit (3), Imroj (1), Mili (10), Arno (9), Majuro (13), Ailinglapalap (2), Lib (1), Kwajalein (2), Mejit (1), Rongelap (1), Taka (1), Eniwetok (6)

*Caroline Islands*

Truk (1), Ponape (1)

*Japan*

Chiba Prefecture (37), Tokarada (1), Muroran-shi (1)

*Russia*

Severo Kurilsk (1), Ozernyi Cape (1), Kamchatka (11), Ilpyr (2), Korf (2), Olyutorka (1), Pahachi (1), Beringovskii (2), Providenya (1), Uelkal (1), Lavrentiya (1), Cape Schmidt (3), Vyvenka (1), Magadanskaya (2), Konergino (1)

*At sea*

55° 50′ N, 164° 20′ W; 25° 03′ N, 179° 56′ E.

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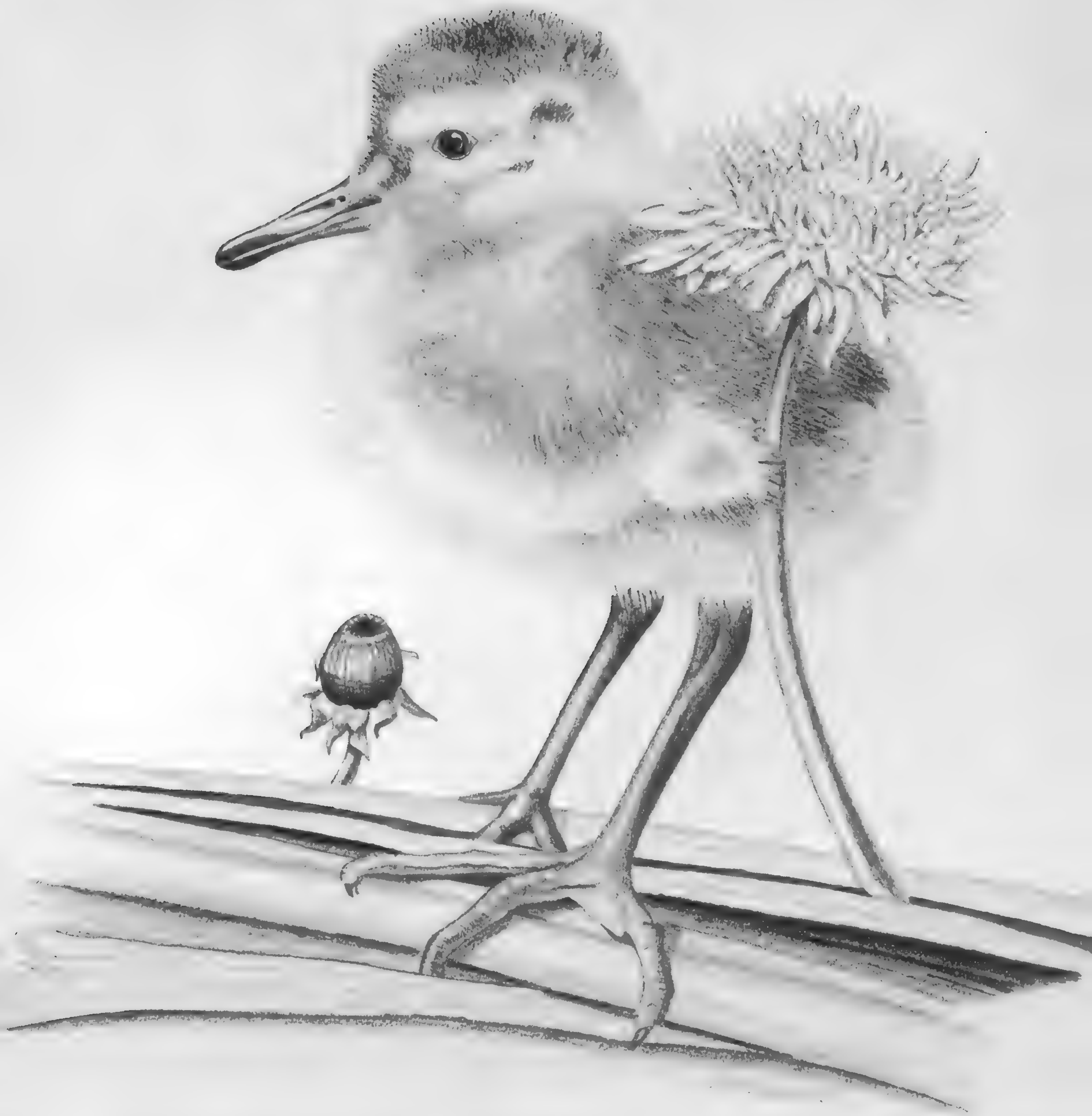

Bar-tailed Godwit, *Limosa lapponica*. Drawing by John Wiessinger.

# NESTING AND SURVIVAL IN A POPULATION OF FLORIDA SCRUB JAYS

GLEN E. WOOLFENDEN

Few long-term studies of avian breeding populations beyond annual censuses exist. Recently, Lack (1966) identified only 12 investigations based on four or more consecutive years of field work. None of the five passerine species included was a corvid.

This report on reproduction in the Florida Scrub Jay (*Aphelocoma c. coerulescens*) is based on observations at 130 nests and monthly censuses of virtually all of the individuals associated with these nests. I conducted all field work at the Archbold Biological Station located eight miles south of Lake Placid in Highlands County, Florida. Field observations began in 1969 when I found eight nests; the sample now includes 25 nests from 1970, 43 from 1971, and 54 from 1972. The number of families under study increased from 1969 to 1971, then leveled off at about 30. What little is known about the breeding of Scrub Jays in Florida appears in Amadon's (1944) important preliminary report based on seven nests and two months of observation.

Florida Scrub Jays possess several behavioral characteristics conducive to a long term study of breeding biology: they are sedentary; they build nests near the ground, and, where unmolested, are very tame. Because of these factors, I have been able to estimate natality and mortality, subjects about which little is known for most birds. As an added inducement, Florida Scrub Jays exhibit cooperative breeding; that is, individuals other than the parents help care for young. "Helpers" have been observed for several species of corvids (Balda and Bateman, 1971; Brown, 1970; Crossin, 1967; Ligon, 1971; Skutch, 1961) but only Grimes (1940) reported them for the Scrub Jay. No detailed study of helpers exists for any bird, however, and thus the effect and source of these altruistic individuals remain largely unknown. I shall reserve this facet of Scrub Jay biology, as well as other aspects of their social organization, for future papers, and will document here some basic aspects of reproduction.

Beginning with nest departure of the young, the typical history of a Scrub Jay that lives for several years is as follows: After fledging in early May, the young remains with the adults for at least one year, during which it assists its parents in the following years' nesting. Some time after one year the bird leaves its parents, forms a permanent and monogamous pair bond, assists its mate in defending a permanent territory, and raises, at most, one brood annually. Rare exceptions are known for most of these generalizations.

Florida Scrub Jays have extremely narrow habitat tolerances, as shown by their overall distribution and their activities at the Archbold Biological Station (hereinafter referred to as the ABS). Pitelka's (1951) map suggests Scrub Jays occupy about one-half of the Florida peninsula; but actually, their total range is less than one-tenth of this area (Westcott, 1970). Not only is the total range of the Florida Scrub Jay small, but it consists of scattered, small patches of a specialized habitat perhaps best described as oak scrub, composed of low dense thickets with numerous open, sandy spaces.

At the ABS, five major natural habitats have been described (Layne, unpubl.) and censused for breeding and wintering birds (Woolfenden, 1969, 1970): sand pine scrub, low flatwoods, slash pine-turkey oak association, scrubby flatwoods, and recently burned scrubby flatwoods. Scrub Jays reside in only the last three of these, and have never even been seen in the other two during five years of almost daily fieldwork (Chet E. Winegarner, pers. commun.). The critical factors in the habitats they avoid seem to be abundance of trees and absence of open sandy spaces. Most of the Scrub Jay families I am following reside in the recently burned scrubby flatwoods, which is shown in Figures 1 and 2. Here Scrub Jays avoid the low, grassy patches (scattered pale areas in Figure 1) and the small stands of pines. Arbib (1972) justifiably listed the Florida Scrub Jay as endangered, because as man continues to convert open scrub into citrus groves, cattle range, and suburbs, its already limited distribution rapidly decreases.

I have not confined my activities to a fixed number of acres. The information presented below is based on observations of a varying number of Scrub Jay families that comprise part of one contiguous population. By concentrating in one area, I have color-banded virtually every individual. An ever increasing percentage of the population is now of known age and parentage. Many of the 130 nests were built by the same parent, or parents, in successive years. I found most nests during incubation or egg laying, but did not discover five until after hatching; a few others were abandoned before eggs were seen. Thus the various analyses that follow come from different subsamples of the whole.

## *Chronology of Breeding*

At the ABS, nesting of the Florida Scrub Jay occurs from late February to late June (Figure 3). The earliest nest ever recorded with contents contained four eggs on 6 March (1971); however, a nest found on 26 March (1972) contained five young about eight days old, and therefore must have held eggs in February. Since incubation requires 17 days with females laying only one egg each day, the first egg of this nest was laid 25 February and the clutch completed on the 29th. The latest known successful nest fledged young on 19 June (1972). For this nest, incubation began on 17 May. Incubation began later, on 21 and 23 May, for two nests, both of which failed. Bent (1946) lists egg dates for 49 nests from 21 March to 14 June. Assuming the latest of these nests contained fresh eggs when found and was successful, it would have held young until the end of June.

Half the egg dates listed by Bent (1946) fall between 10 and 30 April. The time of completion of the clutch for half of my records (1970–1972)

Figure 1. The recently burned scrubby flatwoods west of the Main Building of the Archbold Biological Station is good habitat for Florida Scrub Jays. Many of the nests used in this study, including the one shown in Figure 4, were located within the area shown here. Photograph by K. William Worden.

falls between 24 March and 23 April. Nests contained the maximum number of eggs on 2 April in 1970 (25 nests) and on 5 April for both 1971 (43 nests) and 1972 (48 nests). The latter date is also the peak day for the three years combined. Figure 3 shows the week of completion of 108 clutches, consisting of 71 first clutches, 32 replacement clutches, and five whose number was not determined. I estimated the dates of completion of the clutch for 67 nests found during incubation.

Fledging dates for 45 successful nests (1970–1972) range from 3 April to 19 June with 19 nests fledging young in April, 24 in May, and only 2 in June. Half the fledging dates fall in a two-week period, 25 April to 7 May, and 90 per cent between 15 April and 25 May.

A good parameter for determining synchrony in breeding is the time-span required for the completion of first clutches within a population. The 71 suspected first clutches (Figure 3) were completed within a 10-week period, from late February to early May, with 90 per cent finished between the second week of March and the second week of April. Breeding experience of the female seems to influence the time of laying, as discussed below, although at present I have too few data to be conclusive.

Florida Scrub Jays are single brooded, but will lay several clutches each year in an attempt to produce that one brood. No third clutches were recorded in 1970, the most successful of three nesting seasons (see nesting success below); but several were discovered in 1971 and 1972, when success was lower. In 1972, the least successful of the three years, one pair produced a fourth clutch, which undoubtedly is a rare event. On two occasions, pairs have renested after the death of their young fledglings, and once, a pair attempted to produce a second brood after the first had successfully fledged and were still alive.

In contrast to the Scrub Jay, the breeding season of the Blue Jay (*Cyanocitta cristata*) in Florida is 50 per cent longer, and includes the regular production of two broods. Both jay species begin nesting about the same time, but Blue Jays continue to breed throughout the summer (Woolfenden and Rohwer, 1969). Bent (1946) reported a Florida Blue Jay nest with eggs on 29 August, and Woolfenden and Rohwer (1969) recorded a clutch completed on 6 August (1963).

## *Speculations on the Phenology of Breeding*

The duration of breeding by Florida Scrub Jays correlates closely with certain phases in the annual cycle of the common oak species, all of which, somewhat misleadingly, are considered evergreen. Myrtle and live oak (*Quercus myrtifolia* and *Q. virginiana,* respectively) drop virtually all of their leaves and replace them during a short time in early spring, while the less common Chapman oak (*Q. chapmanii*) undergoes almost simultaneous leaf replacement about a month later. For all three oaks, loss of leaves is followed immediately by flowering and the development of new foliage. Acorns first appear in August on all three species and typically are most abundant in September and October.

Evidence that the foliage condition affects the time and location of nest building comes from the plants chosen as nest sites during various times of the year and from the existence of nests that are deserted. Scrub Jay nests rarely contain eggs before the second week of March (Figure 3), and four of the six nests with clutches completed prior to mid-March were built in true evergreens, instead of the oaks they usually prefer. Jays built three in orange trees (*Citrus* sp.), and the fourth in saw palmetto (*Serenoa repens*). Only four jay nests were built in the late-blooming Chapman oak, and all four held replacement clutches. The earliest of these nests did not hold an egg until 23 April, and the other three did not contain eggs until May.

Scrub Jays vigorously defend their nests when they contain eggs or young, but also for several days after fledging or when they have lost eggs or young to predation. Yet, in the territories of established pairs, I found a few recently-completed nests unattended, including one that contained two uncracked eggs. These unattended nests had one obvious characteristic in common; all were extremely exposed by spring leaf-fall. I suspect exposure following nest construction, or, in at least one case, egg-laying, resulted in these nests being abandoned. If more Scrub Jays bred earlier, desertion of nests would increase because of exposure due to spring leaf-fall.

The appearance of small insects, which form the bulk of the diet of young nestlings, probably is more important than nest concealment in determining the onset of breeding by Scrub Jays. The flowers and tender new foliage of the abundant oak bushes that attract numerous small insects and their small predators appear in April when hatching first becomes abundant. Balda (1970) theorizes that the spring leaf-fall of certain live oaks in two habitats in southwestern United States affects breeding bird densities and nest-site selection. In Florida, I suspect that spring leaf-fall affects nest-site selection and also the annual initiation of breeding in Scrub Jays.

Virtually all Florida Scrub Jays terminate nesting activities by the end of May (Figure 3), two months earlier than Blue Jays and several other Florida passerines (Woolfenden and Rohwer, 1969). This early cessation of breeding may be related to the weak flying powers of Scrub Jays (Amadon, 1944; Hartman, 1961; personal observation) and their habit of harvesting acorns from an open, seasonally-fluctuating environment. Assuming remigial molt reduces the efficiency of an already weak flier, it is important that Scrub Jays confine much of the three-month process of molt (Pitelka, 1945) to a time when frequent flying is unnecessary and food is abundant. As yet, good data on insect abundance are not available, but it seems safe to assume that insects are most common during the wettest and warmest time of the year, namely late spring and summer. Adult Florida Scrub Jays begin remigial molt in May when most young have fledged and are capable of following the older birds that feed them. Adults complete their molt in August shortly before acorns become abundant. Acorn gathering begins in late summer and continues into the winter. This harvesting is concurrent with, or is followed by, several activities that require frequent flying: territorial defense, which is most active in late summer, late winter, and early spring; nest building; feeding of the incubating female by the male; and the feeding of nestlings and young fledglings.

The local populations of Blue Jays appear as reliant on acorns as Scrub Jays. Yet Florida Blue Jays continue nesting into August, almost three months beyond the termination of breeding by Scrub Jays. As opposed to Scrub Jays, Blue Jays utilize forest habitats that provide an additional, more stable, and perhaps more concentrated source of acorns and insects. Furthermore, Blue Jays are better fliers. Based on the weights of Florida specimens of 100 adult-plumaged individuals of each species (Blue Jay, 75.5 grams; Scrub Jay, 80.2 gm) and wing areas of three adult Blue Jays (275.0 square centimeters, 289.0 $cm^2$, and 294.1 $cm^2$) and two adult Scrub Jays (224.2 $cm^2$, and 245.2 $cm^2$), Florida Blue Jays have less wing loading by 0.8 grams per square centimeter (2.6 $g/cm^2$ vs. 3.4 $g/cm^2$).

## Weather and Breeding

Variation in weather seems to have little affect on the breeding schedule of Scrub Jays. Drought and warm winter temperatures broke long-term records during the field work, but I observed no changes in the time of the laying of first clutches. Rainfall for the 12-month span preceding nesting (May to the following April) and based on 34 years of data averages 142 cm

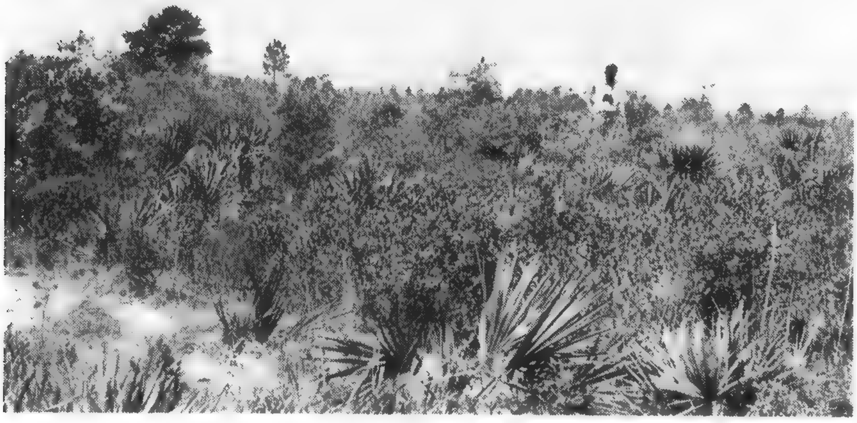

Figure 2. Good habitat for Florida Scrub Jays consists of numerous low oak bushes, scattered palmettos and pines, and many patches of open, bare sand. The nest shown in Figure 4 is in the bush at the author's left hand in this photograph. The breeding female is scolding from the tall bush behind the author. Photograph by K. William Worden.

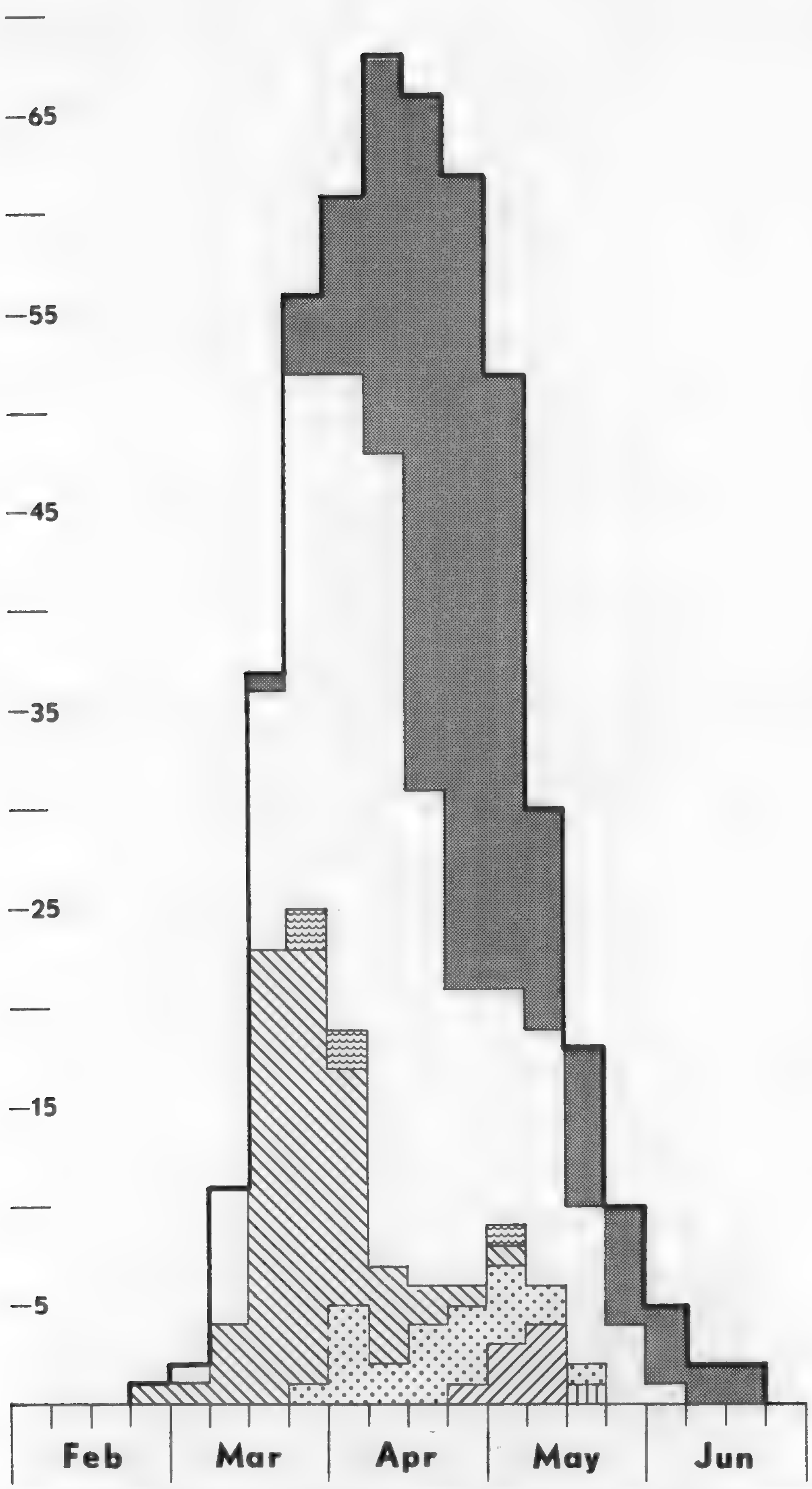

Figure 3. The breeding schedule of Florida Scrub Jays. The heavy outer line shows for each week of the breeding season the number of nests with contents. The diagonal hatching (downward to the right) represents birds with their first clutches of the season (n = 71). The stippled areas represent nests containing second clutches (n = 23). A few nests (n = 8) contained third clutches (diagonal hatching, downward to the left), and one nest (vertical hatching) contained a fourth clutch. Wavy lines represent nests with clutches of unknown history. Shaded portions represent nests containing nestlings.

at the ABS. Rainfall was well above average in 1970 at 174 cm, far below average in 1971 at 80 cm, and also below average in 1972 at 99 cm. In 1970, the many wet-weather ponds in the recently burned scrubby flatwoods were knee-deep in water. The worst drought in 40 years began in August 1970 (Bradley, 1970 and 1971), and the ponds were dry during nesting in 1971. In 1971, myrtle and live oak leaves turned brown, dropped early, and were replaced slowly. Throughout 1972, surface water remained scarce and rainfall was below average for the 11 months before breeding. Drought conditions seemed destined to continue when heavy rains, twice the average amount, fell in April. The oaks responded rapidly with new foliage.

Winter temperatures fluctuate widely. In the winter of 1969–1970, temperatures averaged 2° below normal for December, January, and February. The winter of 1970–1971 was near normal, but warmer temperatures prevailed during the winter of 1971–1972. December 1971 was the warmest in 40 years with an average temperature about 5° C above normal. January temperatures hovered about 4° C above normal while February was near normal.

In summary, weather conditions prior to breeding were wet and cold for 1970, very dry and warm for 1971, and dry and very warm for 1972; yet the onset of breeding by local Scrub Jays was relatively constant. The mean date for the laying of first eggs during the three years varied only six days, from 22 March (1970) to 23 March (1971) to 27 March (1972) for a range of only nine per cent of the time span for laying first clutches. The date when eggs were most numerous varied only four days for the three seasons. The dates on which the first eggs of the season were laid by the same females during different years also shows no correlation with weather even though variation exists. The egg dates for Florida Scrub Jays listed in Bent (1946) range from 21 March to 14 June, which suggests that the time of breeding throughout Florida in years past has been similar to that at the ABS from 1970 to 1972.

Food supply affects the breeding by Piñon Jays (*Gymnorhinus cyanocephalus*) in New Mexico (Ligon, 1971), in that the quantity of piñon pine (*Pinus edulis*) nuts produced in the fall determines the time of breeding during the next year. In 1969, following a crop failure in 1968, Piñon Jays delayed almost all breeding until August and September, at which time a bumper nut crop became available, as well as many insects for feeding to the young. I suspect acorns and insects are necessary for Scrub Jay breeding, but that the oaks are less prone to crop failure than piñon pines and thus do not cause irregularity in the species' breeding schedule.

## *Nesting*

### Nest Site

Florida Scrub Jays build their nests low in a dense bush (Figure 4). Despite the open habitat, they are difficult to detect. Typically, this jay places its nest either in an isolated bush or on the edge of a coppice adjacent to open ground. The 130 active nests I found from 1969 through 1972 include virtually all nestings of about two dozen pairs for the last three years; therefore, the sample probably typifies breeding by Florida Scrub Jays.

The 130 nests observed were built in 13 species of plants. Pitelka (1951), who summarized the important references on nest location, states that

Florida Scrub Jays nest most commonly in oaks and myrtle, and occasionally in rose thickets, grapefruit trees, wax myrtle, wild olive, dwarf holly, jasmine vines, and sand pines. Amadon (1944) found seven nests at the ABS in March and April 1943, of which five were in wax myrtle (*Myrica cerifera*), one in dwarf holly (presumably *Ilex opaca*) and one on a fence in jasmine (*Jasminum* sp.). Wax myrtle still is common at the ABS in the disturbed areas along the roads and fences where Amadon concentrated his observations; but this plant is rare in the more natural habitats.

The list below gives the frequency of distribution of the plants in which I found the 130 nests of the Florida Scrub Jay:

Live oak (*Quercus virginiana*) — 54, including 4 mixed with green brier (*Smilax auriculatus*), 3 each with saw palmetto (*Serenoa repens*) and Spanish moss (*Tillandsia usneoides*), and one each with rosemary (*Ceratiola ericoides*) and crookedwood (*Lyonia ferruginea*); myrtle oak (*Quercus myrtifolia*) — 43, including 3 mixed with green brier, 2 with saw palmetto, and one each with Spanish moss and muscadine grape (*Vitis rotundifolia*); Chapman oak (*Quercus chapmanii*) — 4, including one mixed with crookedwood and hidden by Spanish moss; rosemary — 4; saw palmetto — 4; crookedwood — 3; sand pine (*Pinus clausa*) — 3; fetterbush (*Lyonia lucida*) — 2, including one mixed with dead myrtle oak; scrub holly (*Ilex opaca*) — 1; wax myrtle (*Myrica cerifera*) — 1, covered with woodbine (*Parthenocissus quinquefolia*) and muscadine grape; bamboobrier (*Smilax laurifolia*) — 1, supported by a dead turkey oak (*Quercus laevis*); hickory (*Carya floridana*) — 1, which was bent parallel to the ground by, and intertwined with, the limbs of a fallen dead sand pine; orange trees (*Citrus* sp.) — 7, in orange groves; intertwining branches of live and myrtle oak — 1; intertwining branches of myrtle oak and crookedwood — 1.

## Nest Height

Pitelka (1951) lists a range of nest heights from 0.5 to 3.5 meters. Amadon's (1944) seven nests ranged from 1.2 to 2.8 m (mean 1.7, mode 1.2). Based on estimates made to the nearest quarter meter, 129 of 130 nests found at the ABS were between 0.5 m and 2.5 m from the ground, with one additional nest in a myrtle oak at 4 m. For the entire sample, the mean is 1.2 and the mode 0.8. The average height of the vegetation in the habitat occupied by different families affects the height of the nest from the ground. The shrub layer of the slash pine-turkey oak association and scrubby flatwoods is dense up to 3 or 4 m, and here the mean heights of Scrub Jay nests are 1.7 m and 1.4 m, respectively. In the recently burned scrubby flatwoods at the ABS, only a few patches of live oaks attain these heights. Most of the shrubs are less than 1.5 m tall. Here, jays nest at an average height of 0.9 m. Mature citrus trees with densely foliated, twiggy branches throughout, appear to provide good nest sites from ground level up to about 5 m and thus provide a test situation for optimum nest height. The eight nests built in citrus ranged from 1.4 to 2 m with a mean of 1.6 m.

## Nest-site Preference

The preference by Florida Scrub Jays for certain plants as nest sites may be measured by comparing the percentage of nests in a particular shrub species with the percentage of the total shrub area occupied by that species (Table 1). Jays nest in three of the five habitats at the ABS; the slash pine-turkey oak, the scrubby flatwoods, and the recently burned scrubby flatwoods (Woolfenden, 1969). Susan C. White and James N. Layne kindly made their unpublished notes on the vegetation of two of these habitats available. Their analyses of the shrubs, trees, and herbs were made in

Figure 4. A breeding male Florida Scrub Jay defends his nest in a myrtle oak. The nest's outer shell of oak twigs and the jay's black mask and pale crown help conceal both in the labyrinth of twigs. Photograph by K. William Worden.

randomly chosen quadrats. Scrub Jays nested only in the shrub layer, which they defined as all woody vegetation from one to ten feet high; I considered only this component of the vegetation in the comparisons that follow. White and Layne estimated the percentage of the shrub element occupied by each species of plant by multiplying the relative density of a species by its mean radius. I used these dominance figures to calculate percentage of the shrub layer occupied by each species. For the recently burned scrubby flatwoods habitat, which was not included in their analysis, two transects totalling 300 m were established by choosing random starting points and compass directions within the tract occupied by marked Scrub Jay families. I measured the amount of ground below the transect line covered by each shrub to calculate the percentage of the total shrub area occupied by each plant in the habitat. In all three habitats at least 77 per cent of the area occupied by shrubs supports four: myrtle oak, live oak, saw palmetto, and sand palmetto (*Sabal etonia*). Only six other plant species comprise one or more per cent of the shrub layer in any of the habitats; Table 1 lists all of these, including gallberry (*Ilex glabra*) and tarflower (*Befaria racemosa*), not mentioned elsewhere in the text.

Florida Scrub Jays living at the ABS strongly prefer live oak as a nest site. This is shown clearly by comparing the percentage of the shrub layer occupied by each plant species with the percentage of the nests it supports (Table 1). The jays probably prefer the live oak because of its numerous, stiff, divergent twigs. The differences in degree of preference in the three habitats, weakest in the slash pine-turkey oak association and strongest in

TABLE 1

Scrub Jay Nest-site Preferences in Three Habitats at the Archbold Biological Station

| | *Slash pine-turkey oak* | | *Scrubby flatwoods* | | *Recently burned scrubby flatwoods* | |
|---|---|---|---|---|---|---|
| *Species* | *Percentage of shrubs* | *Percentage of 11 nests* | *Percentage of shrubs* | *Percentage of 46 nests* | *Percentage of shrubs* | *Percentage of 65 nests* |
| Live oak (*Quercus virginiana*) | 16 | 27 | 15 | 50 | 4 | 42 |
| Myrtle oak (*Q. myrtifolia*) | 21 | 55 | 31 | 37 | 32 | 31 |
| Chapman oak (*Q. chapmanii*) | 9 | — | 7 | — | 2 | 6 |
| Rosemary (*Ceratiola eriocoides*) | 0 | — | 0 | — | 0 | 6 |
| Sand pine (*Pinus clausa*) | 0 | — | 0 | — | 0 | 5 |
| Crookedwood (*Lyonia ferruginea*) | 4 | — | 2 | 4 | 1 | 3 |
| Fetterbush (*L. lucida*) | 0 | — | 9 | — | 3 | 3 |
| Saw palmetto (*Serenoa repens*) | 31 | — | 21 | 7 | 41 | 1 |
| Sand palmetto (*Sabal etonia*) | 9 | — | 10 | — | 10 | — |
| Gallberry (*Ilex glabra*) | 0 | — | 0 | — | 5 | — |
| Tarflower (*Befaria racemosa*) | 0 | — | 0 | — | 2 | — |
| Turkey oak (*Quercus laevis*) | 9 | — | 0 | — | 0 | — |
| Scrub holly (*Ilex opaca*) | 0 | — | 0 | 2 | 0 | — |
| Totals | 99 | 82* | 95 | 100 | 100 | 96* |

*Two nests are deleted from the slash pine-turkey oak analysis, one in a hickory bent parallel to the ground and intertwined with limbs of a dead, fallen sand pine, and one in a tangle of bamboobrier suspended by a dead turkey oak; and two are deleted from the recently-burned scrubby flatwoods, one in mixed myrtle oak and live oak and one in mixed myrtle oak and crookedwood.

the recently burned scrubby flatwoods, probably are related to the local presence of two forms of myrtle oak. One form has smaller leaves with narrower bases and more numerous twigs, whereas the other has larger broader-based leaves and fewer twigs. The latter form may be the *Quercus inopina* of Ashe referred to by Small (1933) under *Q. myrtifolia.* In the slash pine-turkey oak habitat, most myrtle oaks are the typical *"myrtifolia"* form where I found all six jay nests in this habitat. In the scrubby flatwoods, both forms of myrtle oak occur commonly, thus providing a test area for preference for one or the other as a nest site by Scrub Jays. Here 12 of 17 myrtle oak nests were in the *"myrtifolia"* form. Thus, the increasing preference for myrtle oak as one traverses from recently burned scrubby flatwoods through scrubby flatwoods to slash pine-turkey oak, and the concomitant decreasing use of live oak, parallels an increase in abundance of the twiggier *"myrtifolia"* form, which more closely resembles live oak.

Rosemary and sand pines with low limbs provide suitable nest sites, but both plants are scarce locally in the habitats occupied by Scrub Jays. The abundant saw palmetto rarely is used. Three of the four nests housed in saw palmetto were built by the same pair, and two of these were in different parts of the same clump in successive seasons. Sand palmetto forms thick clumps less often than saw palmetto and thus is even less suitable to the jays.

### Nest Construction

Although I have few data on nest building, my observations support Amadon's (1944) conclusions that both members of the pair construct the nest, that they never use material from old nests, and that completion requires about five days. In addition, Scrub Jays never re-use nests and they do not make incomplete nests, as do Blue Jays (Hardy, 1961). Only the breeding pair builds, which is not true for its congener, the Mexican Jay (*Aphelocoma ultramarina*) in which the entire flock may participate (Brown, 1970). Most of the twigs appear to be taken directly from shrubs, as opposed to being picked up from the ground. Old nests disintegrate slowly, and those from several previous years exist in established territories.

### Nest Materials

Florida Scrub Jays build a typical corvid nest, an open bulky structure of course outer twigs. Virtually all the sticks in the outer shell come from oaks, including those used in nests built in citrus groves. A few rootlets and finer sticks from a variety of plants, including sand pines and vines, are covered by the firm lining which is made almost entirely from the tough fibers of sand palmetto. Unlike Blue Jays (Hardy, 1961), Scrub Jays do not use paper or other foreign material.

### Interval between Building and Egg-laying

As is typical of many birds (Van Tyne and Berger, 1959), the time between completion of a nest and the laying of the first egg is longer for the first nesting of the year, and especially an early first nesting, than for renestings. Two nests completed in late February did not have eggs until approximately 15 and 17 days later. Another first nest of the season was completed about 25 March and did not contain an egg until about 9 April. This is late in the year for a first nesting, but both members of the pair were only two years old and breeding for the first time. The interval between failure of one nest and the subsequent attempt to re-lay eggs usually is less than two weeks and is known to have been as short as eight days.

## Egg-laying and Incubation

Of 101 Scrub Jay nests seen with eggs attended by adults, I found 34 before the clutch was complete; however, only one was visited daily. The results, although limited, indicate that Scrub Jays normally lay one egg each morning, as is typical of passerines (Thomson, 1964), that incubation typically begins after most of the eggs in the clutch have been laid, that only females incubate (Amadon, 1944), and that incubation requires about 17 days (Bent, 1946).

Amadon's (1944) suggestion that Scrub Jays begin incubation with the first egg seems incorrect. On numerous occasions, when I visited nests during egg-laying, I found the eggs cold and wet from dew or rain; and on one occasion an egg marked with ink lost its number during a thundershower that occurred shortly after marking. Scrub Jays dash to their nests and crouch over their incomplete clutches when humans come near. I suspect this behavior resulted in the conclusion that incubation begins with the first egg. Frequently, I saw both Scrub Jay parents away from their nest and eggs. When they saw me, they dashed for the unattended nest. Upon my arrival at the nest, one, or sometimes both, was sitting over the eggs in a characteristic defensive posture (Amadon, 1944). On such occasions, when I lifted the defender from an incomplete clutch, the eggs still were cold and sometimes wet.

Amadon (1944) correctly concludes that only female Scrub Jays incubate. The statement to the contrary by Grimes in Bent (1946), which probably was written before Amadon's paper appeared, most likely originates from observing nest-defense behavior by the male. The estimate of 17 days for incubation given in Bent (1946) may be based on Grimes' observation of one nest in which the fifth and last egg was laid on 1 April. The three eggs hatched the night of 16 to 17 April. Jinny Emlen and I found a nest with one egg on 2 April and observed it each day until after hatching. The fourth and last egg appeared the morning of 5 April. Hatching of the first egg occurred between 17:00 on 21 April and 07:30 on 22 April, the second by 14:30 on 23 April, at which time the third and final egg to hatch was pipped. This egg hatched before 07:30 on 24 April (all E.S.T.). Assuming incubation began with the last egg of the clutch, the duration was 17 to 19 days. Five other nest histories, each with a different female, but all less detailed, suggest that incubation lasts between 16 and 19 days. These and many other nests document frequent and considerable variation in the time of hatching of eggs in the same clutch. Intermittent sitting on the eggs prior to completion of the clutch might account for some of the variation.

The date of laying of the first egg of the season varies with the breeding experience of the female. The average laying date for females that have nested one or more years was 20 March. For seven females breeding for the first time, the average date was 31 March. This 11-day delay amounted to 11 per cent of the laying season (Figure 3). If the dates for laying the first egg by five females, suspected of breeding for the first time, are added to the sample, the average date becomes 5 April, for a total delay of 18 per cent of the laying season. The five females suspected of breeding for the first time were aged by the appearance of the primary coverts (Pitelka, 1945) and/or by having been unpaired helpers the previous breeding season. The onset of breeding also seemed to vary with the time when pairing occurred and a territory was established during the previous 12 months, but insufficient data are available at present for analysis.

The average time between the failure of one breeding attempt and the laying of the first egg for the next attempt in the same season was 12 days ($n = 28$). With the few data thus far obtained, I could find no correlation between this time span and the time of the year, the number of clutches laid, or the state in the breeding cycle at which failure occurs. Possibly these and other factors interact in ways that obscure the individual relationships. The shortest span, six days, occurred following failure during laying, and the longest span, 20 days, occurred with a pair whose fledglings died within about one week after leaving the nest. About 12 days elapsed between the fledging of young and the laying of the first egg for the one pair that attempted a true second brood.

## Clutch Size

The mean clutch size for the 101 Scrub Jay nests found during incubation, or during laying and lasting into incubation, was 3.4. Five nests contained two eggs, 49 held three eggs, 46 had four eggs, and one had five eggs. Clutch size for Florida Scrub Jays varies from three to five according to Bendire (1895), and according to Howell (1932), from two to four. Clutches of both five eggs and two eggs occur at the ABS, but they are rare. In addition to the one five-egg clutch listed above, Grimes (*in* Bent, 1946) reported one nest with five nestlings and I have seen two such nests. Proving the existence of clutches of less than the average size is difficult, because it is virtually impossible to know that the female laid only the number of eggs found in a nest. Some authors delete small clutches from an account of clutch size, although no evidence for egg loss may exist. Circumstantial evidence suggests that the five two-egg clutches I found are valid. Two of these were found during egg-laying, and two others within three days after the onset of incubation. Four of the five reached the hatching stage, even though Scrub Jay nests that exhibit a partial loss of eggs are less likely to reach the hatching stage (67%) than those for which partial egg loss is not recorded (81%). First breeders of some bird species lay smaller than average clutches; I have documented this for Scrub Jays. Old individuals of some species also lay smaller than average clutches. Two of these five two-egg clutches were laid by first breeders, and a female at least 11 years old laid another.

Most single-brooded species lay smaller replacement clutches than first clutches of the season (Klomp, 1970; Lack, 1954). In Scrub Jays, however, second (replacement) clutches are larger than first ones (Table 2), and these differences are significant at the five per cent level (one-tailed t-Test). The data on third and fourth (replacement) clutches are few and were not tested. Animal food appears to increase as the breeding season progresses, and this may account for larger replacement clutches.

Clutch size increases with the female's breeding experience (Table 3). I compared the clutch sizes of third-year and later breeders with first-year breeders and with first- and second-year breeders combined, and the differences were significant at the one per cent level (one-tailed t-Test). Information not given in Table 3 includes the facts that nine females produced the

TABLE 2

Clutch Size and Seasonal Clutch Number

| *Number of eggs per clutch* | *Seasonal clutch number* | | | |
|---|---|---|---|---|
| | *1st* | *2nd* | *3rd* | *4th* |
| 2 eggs | 5 | 0 | 0 | 0 |
| 3 eggs | 35 | 9 | 3 | 1 |
| 4 eggs | 28 | 13 | 2 | 0 |
| 5 eggs | 0 | 1 | 0 | 0 |
| Total number of nests | 68 | 23 | 5 | 1 |
| Mean | 3.3 | 3.6 | | |

13 first-season breeding records, and that these include nine first clutches of the season, three second seasonal clutches, and one third. The one four-egg clutch in the total of 13 was a second attempt during the female's first season. The one female that delayed breeding until three years of age laid the one two-egg clutch.

Field work has not lasted long enough to test for a diminution in clutch size with increasing age of females, although the fact that the only known old female in the population (minimum age of 11 years) produced a two-egg clutch suggests that such an inverse relationship might exist.

## *Reproductive Success*

An important goal in the study of reproduction is to establish the rate at which breeding adults are added to the population. Then, if the mortality rate of breeding adults can be determined, one can make predictions regarding population turn-over. Scrub Jays possess several traits that simplify the study of natality and mortality; however, now it is known that many individuals reach the minimum reproductive age of two years but do not breed. The status of these individuals must be understood to measure productivity accurately.

The percentages of nests that fledge young, of eggs laid that hatch, and of nestlings that fledge are less accurate measures of the early stages of reproduction than the number of fledglings produced per breeding pair. Many studies report these parameters, but stop at this point in the reproductive cycle because the young of many birds cannot be followed after they leave the nest (*e.g.* Lack, 1953). To make my data comparable to these studies, I include similar analyses for the Florida Scrub Jay.

### Partial Losses of Clutches and Broods

The probability that a nest will remain active into the next stage in the breeding cycle (hatching for eggs, fledging for nestlings) decreases once the nest loses some of its contents. Only 8 of 13 nests known to have experienced a partial loss of eggs reached hatching (61%), whereas 61 of 75 nests whose contents remained intact, reached the hatching stage (82%). Only 10 of 15 nests that lost some nestlings fledged any young (67%), whereas 45 of 58 nests in which no young were known to have been lost were successful (78%). Probably other nests experienced partial losses which remained undetected prior to total failure; therefore, the differences in success between nests suffering partial loss versus nests not suffering partial loss may be even greater than the percentages show.

### Predation of Eggs and Nestlings

Although about 64 nests were robbed of all their eggs or young, and about 15 more experienced partial loss, I have few facts regarding the causes of nest predation. Loss of nest contents because of desertion occurred only a few times. In one case a female deserted after losing her mate; but in all other cases I saw both parents after predators robbed their nests. In about three instances, exposure of the nest seemed to cause desertion. Signs of disturbances included nest linings in disarray at several robbed nests, a few of which also were tipped or flattened. In two instances, the incubating female was killed. At all the other nests, which is about 90 per cent of the sample, I detected no signs of disturbance other than the loss of contents.

Several predatory mammals and large snakes are common at the ABS, and no doubt some eat Scrub Jay eggs and nestlings, but I suspect that Fish Crows (*Corvus ossifragus*) are among the most frequent nest robbers. Blue Jays probably take few Scrub Jay eggs and nestlings, for they only infrequently venture out into the most open of Scrub Jay habitats, and quickly retreat in the presence of Scrub Jays. Fish Crows breed at the ABS, and have been seen there flying with nestling passerines dangling from their bills, although none of these were identified as Scrub Jays.

Two observations support my suspicion that Scrub Jays sometimes rob nests of their own species. During the brief time required to band an incubating female that I had lifted from a nest, two of her three eggs disappeared. Only the breeding male and his brother were known to be near the nest, two meters from where I stood. After I discovered the eggs were missing, I noticed that the unmated male's bill glistened with moisture. In the second observation, a helper male invaded an adjacent territory and fought with the brooding female in what appeared to be an attempt to dis-

TABLE 3

Clutch Size and the Breeding Experience of Females

| | *Breeding Experience* | | |
|---|---|---|---|
| *Number of eggs per clutch* | *First attempt* | *Second attempt* | *Third and later attempts* |
| 2 eggs | 2 | 0 | 0 |
| 3 eggs | 10 | 5 | 8 |
| 4 eggs | 1 | 0 | 7 |
| 5 eggs | 0 | 0 | 1 |
| Number of clutches | 13 | 5 | 16 |
| Mean clutch size | 2.9 | 3.0 | 3.6 |

TABLE 4
Reproductive Success by Florida Scrub Jays (Based on 7 females breeding three successive years, 14 females breeding two successive years, and 28 females breeding one year)

| *Breeding stage* | *Year*<br>*1970* | *1971* | *1972* | *Total* |
|---|---|---|---|---|
| 1 Number of pairs that nested* | 18 | 28 | 31 | 77 |
| 2 Number of nests completed | 24 | 42 | 50 | 116 |
| 3 Number of nests with eggs | 23 | 41 | 48 | 112 |
| 4 Number of nests with complete clutches | 23 | 36 | 45 | 104 |
| 5 Number of nests with nestlings | 19 | 26 | 25 | 70 |
| 6 Number of nests that fledged young** | 16 | 18 | 14 | 48 |
| 7 Number of fledglings produced | 47 | 48 | 33 | 128 |
| Average number of nests per pair (2/1)*** | 1.3 | 1.5 | 1.6 | 1.5 |
| Average number of fledglings per pair (7/1) | 2.6 | 1.7 | 1.2 | 1.7 |
| Average number of fledglings per successful pair (7/6) | 2.9 | 2.7 | 2.4 | 2.7 |
| Percentage of pairs fledging at least one young (6/1) | 89 | 64 | 42 | 62 |
| Percentage of nests with eggs fledging at least one young (6/3) | 70 | 44 | 29 | 43 |
| Percentage of nests with completed clutches fledging at least one young (6/4) | 70 | 50 | 31 | 46 |

*In 1972 one additional pair did not nest.
**In 1972 two sets of fledglings were produced by one pair.
***Numbers in parentheses refer to breeding stages.

lodge her from the nest that contained two young. The male was unsuccessful and retreated after a brief, but severe, fight.

On occasion, I suspect that Scrub Jays are robbed by predators that could have been driven off, except that all jays were away from the nest simultaneously. A few times I arrived at a nest before any Scrub Jay appeared. The frequent partial loss of eggs or nestlings may be caused by predators chased from the nest before they completely remove its contents.

## Hatching Failure

Of 211 eggs in 67 nests that remained intact long enough for hatching to occur, 16 failed to hatch. Frequently, the unhatched eggs, left in the nest through one or more weeks of the nestling stage, became buried in the fibers of the nest lining. A hatching failure of 7.6 per cent only slightly exceeds that reported for two other open-nesting passerines, the Song Sparrow (*Melospiza melodia*) with 6.1 per cent (Nice, 1937), and the Cedar Waxwing (*Bombycilla cedrorum*) with 4.6 per cent (Putnam, 1949). Grimes (*in* Bent, 1946) suggests a much higher hatching failure in Florida Scrub Jays with his statement "I have never known all the eggs to hatch in a set of Scrub

Jay." If taken literally, this would constitute a hatching failure of 25 per cent or more. Many of his observations were made near Jacksonville, Florida on the remnants of a population disappearing because of habitat destruction. Grimes (1940) wondered if inbreeding might have caused the low hatching success.

### Nesting Success

Nesting success for the Florida Scrub Jay population at the ABS is 43 per cent for the three years 1970–1972 combined (Table 4), when calculated by the number of nests fledging at least one young divided by the number of nests containing eggs. Nice (1957), summarizing 35 major studies of open-nesting altricial birds, recorded 49 per cent. However, since then, several authors have suggested that the customary method biases the results toward higher success (Mayfield, 1961; Skutch, 1966; Woolfenden and Rohwer, 1969), and detailed studies have given lower rates (Nolan, 1963; Snow, 1955). Even the figure of 43 per cent for Florida Scrub Jays probably is slightly higher than the actual percentage of success, because a few nests with eggs probably are never found. Compensating in part for this would be those nesting attempts deemed failures in which fledging occurred, but the young died before being detected.

Florida Scrub Jays produce only one brood each year and fledglings are rather easy to locate in the population at the ABS; therefore, an internal check on the percentage of nesting success is made by dividing the percentage of pairs producing fledglings (62) by the average number of nests with eggs produced per pair (1.5). The result (41%) is similar to, but slightly lower and probably more accurate than, the 43 per cent obtained by the customary procedure.

### Hatching and Fledging Success

Hatching success, or the number of eggs laid that produce nestlings, based on a sample of 357 eggs, is 52 per cent (Table 5); Nice (1957) obtained 60 per cent for a large variety of open-nesting altricial birds. Fledging success, or the number of eggs laid that produce fledglings, for the same 357 Scrub Jay eggs, is 32 per cent; Nice had a considerably higher percentage (46) from her sample. I suspect that both my results and Nice's are biased toward higher success, because of the inclusion of eggs found near the time of hatching. My figures for Scrub Jays are perhaps less biased than for the numerous studies she analyzed, because I probably found more nests earlier in the nest cycle.

The production of fledglings varied widely for the three seasons. I suspect that predation and weather conditions, acting directly or indirectly through starvation, caused the variation. Nest success was highest in 1970 (70%), a wet year, intermediate in 1971 (44%), a drought year when at least a few nestlings starved, and lowest in 1972 (29%), when drought conditions continued, although perhaps less severely, and when predation seemed greatest.

The number of renestings was greater during years of lower nesting success. In 1970, when nest success was highest, only 29 per cent of all nests represented second and third attempts of the season. In 1971, with intermediate nesting success, 33 per cent of the nests represented second and third attempts. Success was lowest in 1972, when 45 per cent of the nests were second and third (and one unique fourth) attempts.

TABLE 5

Survival of Florida Scrub Jay Eggs

| *Breeding stage* | *1970* | *1971* | *1972* | *Totals* |
|---|---|---|---|---|
| 1 Total number of eggs | 77 | 129 | 151 | 357 |
| 2 Number of eggs in completed clutches | 75 | 123 | 144 | 342 |
| 3 Number of eggs remaining at hatching time | 57 | 79 | 78 | 214 |
| 4 Number of nestlings | 51 | 72 | 64 | 187 |
| 5 Number of fledglings | 40 | 48 | 27 | 115 |
| Percentage of eggs producing nestlings (4/1)* | 66 | 56 | 42 | 52 |
| Percentage of eggs producing fledglings (5/1) | 52 | 37 | 18 | 32 |

*Numbers in parentheses refer to breeding stages.

As shown in Table 6, replacement clutches show a lower probability of producing fledglings than first clutches, and this phenomenon held true for each of the three years. An analysis of nesting success through the breeding season was not made; however, the usual pattern that shows a decrease in success as the season progresses appears to exist, in part at least, because success decreases sharply from first clutches to replacement clutches.

### Fledglings Raised per Breeding Pair

For the three seasons combined, the ABS Florida Scrub Jays produced 1.7 fledglings per pair, or 85 per 100 breeding adults. Annual production varied directly with nesting success, ranging from 2.6 fledglings per breeding pair in 1970 to 1.2 in 1972 (Table 4).

### Survival of Fledglings

Florida Scrub Jays typically remain in their natal territory for more than a year after fledging. Of the 53 individuals followed from fledging to one year of age, only two departed; and of the 90 birds followed for varying lengths of time up to 11 months, none of these departed either. These 90 apparently died, since they were never seen again in a large area where frequent observations were made over many years. Other evidence suggesting that fledglings (here defined as individuals that have left the nest but are less than one year old) have a strong tenacity for the natal territory is that unmarked individuals rarely appear in the study tract from regions beyond. Those few young that wandered into established territories from known natal sites always were chased back home. The two fledglings that permanently left their natal territory were siblings, and they departed at the age of 11 months when an aggressive male replaced their missing father.

The sedentariness of fledgling Scrub Jays allowed me to estimate their survival by direct observation of marked birds. I followed 143 individuals

## TABLE 6

### Nesting Success of Florida Scrub Jays Related to Seasonal Clutch Number

|  | *Seasonal clutch* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | *First* |  |  |  | *Second* |  |  |  | *Third* |  |  |  | *Fourth* |  |  |  | *All clutches* |
| *Breeding stage* | 1970 | 1971 | 1972 | All | 1970 | 1971 | 1972 | All | 1970 | 1971 | 1972 | All | 1970 | 1971 | 1972 | All | All years |
| 1 Number of nests with eggs | 15 | 27 | 29 | 71 | 6 | 9 | 13 | 28 | 0 | 4 | 5 | 9 | 0 | 0 | 1 | 1 | 109 |
| 2 Number of nests with complete clutches | 15 | 25 | 28 | 68 | 6 | 7 | 13 | 26 | 0 | 4 | 3 | 7 | 0 | 0 | 1 | 1 | 102 |
| 3 Number of nests that fledged young | 12 | 15 | 10 | 37 | 2 | 2 | 3 | 7 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 46 |
| 4 Percentage of nests fledging young (3/1)* | 80 | 56 | 34 | 52 | 33 | 22 | 23 | 25 | – | 25 | 20 | 22 | – | – | 0 | 0 | 42 |

*Numbers in parentheses refer to breeding stages.

after they fledged (arbitrarily considered to be May in Table 7) and 53 (37%) survived their first year. The percentage of fledglings alive when they became yearlings (here defined as individuals between the ages of one and two years) varied from a low of 27 per cent in 1972 to a high of 47 per cent for 1969; however, the patterns of survival are similar in that most losses occurred sometime during the first seven months, followed by a pronounced leveling off of the survivorship curve.

### Survival of Yearlings

Survival of yearling Florida Scrub Jays also can be estimated by direct observation of marked birds, because dispersal is so limited. Even though Scrub Jays first attain sexual maturity when two years old, many individuals do not breed, but instead remain in their natal territory as helpers. In addition, those that do breed frequently take up stations near their natal territory. Further evidence of only limited dispersal by Florida Scrub Jays comes from the fact that Westcott (1970) banded 230 Scrub Jays two miles south of the ABS in contiguous scrub habitat. Although his field work and mine were contemporaneous for more than a year, neither of us ever saw a marked bird from the other's study tract. During periodic visits to Westcott's study area since his departure, I have never seen a jay banded at the ABS.

TABLE 7

Monthly Survival of Fledgling Florida Scrub Jays

| *Number of months survived* | | *Numbers of individuals and percentage survived** | | | | |
|---|---|---|---|---|---|---|
| | | *1969* | *1970* | *1971* | *1972* | *All years* |
| | Month of fledging: | | | | | |
| | May | 17 (100) | 45 (100) | 48 (100) | 33 (100) | 143 (100) |
| | Months after fledging: | | | | | |
| 1 | June | 14 ( 82) | 33 ( 73) | 36 ( 75) | 23 ( 70) | 106 ( 74) |
| 2 | July | 14 ( 82) | 26 ( 58) | 33 ( 69) | 22 ( 67) | 99 ( 69) |
| 3 | August | 13 ( 77) | 26 ( 58) | 29 ( 60) | 22 ( 67) | 88 ( 62) |
| 4 | September | 13 ( 77) | 23 ( 51) | 24 ( 50) | 18 ( 55) | 78 ( 55) |
| 5 | October | 12 ( 71) | 23 ( 51) | 20 ( 42) | 12 ( 36) | 67 ( 47) |
| 6 | November | 10 ( 59) | 22 ( 49) | 18 ( 38) | 10 ( 30) | 60 ( 42) |
| 7 | December | 10 ( 59) | 21 ( 47) | 17 ( 35) | 10 ( 30) | 58 ( 41) |
| 8 | January | 10 ( 59) | 20 ( 44) | 17 ( 35) | 10 ( 30) | 57 ( 40) |
| 9 | February | 10 ( 59) | 20 ( 44) | 17 ( 35) | 10 ( 30) | 57 ( 40) |
| 10 | March | 10 ( 59) | 19 ( 42) | 17 ( 35) | 10 ( 30) | 56 ( 39) |
| 11 | April | 10 ( 59) | 19 ( 42) | 17 ( 35) | 9 ( 27) | 55 ( 38) |
| 12 | May | 8 ( 47) | 19 ( 42) | 17 ( 35) | 9 ( 27) | 53 ( 37) |

*Percentages appear in parentheses following numbers of individuals.

I followed 44 yearlings, of which 37 (84%) survived to an age of two years. Eight of the 44 jays hatched in 1969, 19 in 1970, and 17 in 1971. Certainly, some of this loss of yearlings (16%) was due to dispersal and not death. In order to adjust the 16 per cent annual loss so that it represents only death, I assumed that dispersal rates are not age-related for unpaired jays two-years old and older, and that immigration equals emigration. About four unmarked Scrub Jays became established within the territories occupied by about 100 known individual jays during each of two years of field work (May 1970 through May 1972), which gives a dispersal rate of about four per cent per annum. Thus, I obtained a final estimate of yearling survival of 88 per cent. Survival of breeding adults was only eight per cent lower than this seemingly high figure, lending support to its accuracy. Heretofore, no passerine was known to have such a high rate of survival (Lack, 1954, 1966).

The earliest permanent dispersal of a yearling occurred at age 14 months, when a male replaced a lost mate in an adjacent territory; but even in this case, the young male frequently visited its natal territory.

## Production of Potential Breeders

Annual production of fledglings (85 per 100 breeding adults), annual survival of fledglings (37%), and annual survival of yearlings (88%) resulted in the production of 27 potential breeders per 100 breeding adults. A comparison of this replacement rate with adult mortality provides an estimation of turn-over in the entire population.

## Survival of Breeding Adults

Established breeders seem to be the most sedentary of all age classes of Scrub Jays. Only two of 93 breeding adults followed for varying lengths of time up to four years, have moved from one breeding territory to another. Thus, the observation of marked birds also seems to provide a reasonable method for estimating the survival of breeding adults.

I followed the 93 known breeders for an accumulated 196 bird-years during which 40 individuals were lost. This gives a mortality rate of 20 per cent per annum. An independent source of information from which I estimated the mortality rate was the history of 24 adult-plumaged Scrub Jays banded at the ABS in the summers of 1959 and 1960. I found two of these marked birds in my study tract when I began field work in 1969, both of which disappeared in 1970. Using 1960 as the year of banding to help compensate for individuals probably banded as yearlings, I estimated an identical mortality rate of 20 per cent per annum.

Using the mortality rate of 20 per cent per year, the average life expectancy for a two-year old, breeding Scrub Jay is 4.5 years, as calculated by the formula $\frac{2-m}{2m}$ where m = percentage of annual mortality. Maximum longevity is much greater, of course, and is known to reach 11 or 12 years. Two jays banded as adults (determined by plumage) at the ABS in May 1960 lived until 1970. One, a male, disappeared in February at a minimum age of 10 years and 9 months. The other, a female, disappeared in July after breeding at a minimum age of 11 years and 2 months. Westcott (1970) reported a 12-year-old female, banded as an adult (how determined was not stated) in the summer of 1960 and still alive the summer of 1970. When last seen, she was at least 12 years old, if her age at banding was determined by breeding status, or perhaps only 11 years old if determined by plumage.

### Population Stability

If the natality (27%) and mortality (20%) rates calculated above are correct, the ABS Scrub Jay population seems to be producing more replacements than are necessary for a stable population. However, an additional factor needs to be included in the calculations, namely, the percentage of adult-age helpers in the population. Many Scrub Jays two-years old and older do not breed, but instead remain as helpers. At present, I assume that helpers increase productivity and, therefore, must be included in the number of individuals contributing to the production of a given number of young.

From 1970 through 1972, 78 breedings were attempted, for which 33 (42%) included adult-aged helpers. Thus, approximately 142 adults, rather than the 100 breeders, produced an average of 27 new adults annually. If we assume that the mortality rate of adult-aged helpers was similar to that for breeders (20% per annum), the annual mortality for the 142 producers was 28 individuals, a figure almost identical to the 27 new potential breeders produced annually. Thus, the population appears to be nearly stable.

## *Summary*

Florida Scrub Jays are sedentary, tame, monogamous, have a narrow habitat tolerance, and exhibit cooperative breeding. Most nesting occurs between mid-March and early June. Hatching follows spring leaf-fall and the blooming of live oak and myrtle oak bushes that dominate in the scarce and scattered habitats to which Florida Scrub Jays are confined. The tender new growth on these oaks attracts numerous small insects which form the bulk of the food brought to young nestlings. The termination of nesting in early summer provides ample time both for bringing fledglings to independency and for the post-breeding molt, which occurs before acorns mature and harvesting becomes a necessary activity.

Florida Scrub Jays prefer live oak and myrtle oak bushes as nest sites. Here they build near an opening in the plant cover about 1.2 meters off the ground. The immediate nest site is among dense twigs. The nest is a bulky structure of course outer sticks with a firm inner lining of palmetto fibers. Only parent Scrub Jays build nests.

Clutches vary from two to five eggs with a mean of 3.4. Clutch size increases slightly from first (3.3) to second (replacement) clutches (3.6) of the season, and also from first breeders (2.9) to third-season and later breeders (3.6). Florida Scrub Jays often lay three clutches to produce one surviving brood of fledglings. Loss of eggs and nestlings occasionally includes Scrub Jays robbing nests of their own species. The frequency of hatching failure appears similar to that of other North American open-nesting passerines. Only females incubate, although males and, at certain stages in the nest cycle, even helpers will crouch over a nest to defend its contents.

Nesting success, calculated in the customary manner, was 43 per cent. Success decreased from 52 per cent for first clutches of the season, to 25 and 22 per cent for second and third (replacement) clutches. Production of fledglings per pair per year for three years, 1970 to 1972, varied from 2.6 to 1.2 with an average of 1.7 (85 per 100 breeders).

Fledglings, defined as individuals that leave the nest but are less than one year old, remained in the parental territory where they helped their parents raise the young of the following year. Survival of fledglings varied from 27 to 47 per cent for four years with an average of 37 per cent.

Yearlings, defined as individuals between ages one and two years, usually remained in their natal territory. Emigration was estimated at four per cent and survival of yearlings at 88 per cent. Breeding first occurred at the age of two years; thus production of potential replacements for the breeding adults was 27 per cent per year (85 × .37 × .88). Many individuals two years old and older did not breed, however. Instead, they continued to reside in their natal territory and assist a breeding pair, which sometimes consisted of individuals other than the helpers' own parents.

Mortality of breeding adults, computed from two separate samples, was a low 20 per cent per year, which was seven per cent less than the number of potential breeders produced each year. However, assuming the helpers found in many of the territories really do help the parents raise their young, then the number of individuals required to raise 27 potential breeders each year averaged out to be 142 instead of 100. Assuming mortality for the helpers was similar to that for breeding adults, 20 per cent per annum, then the number of deaths each year was 28 (142 × .20), which was almost identical to the replacement rate.

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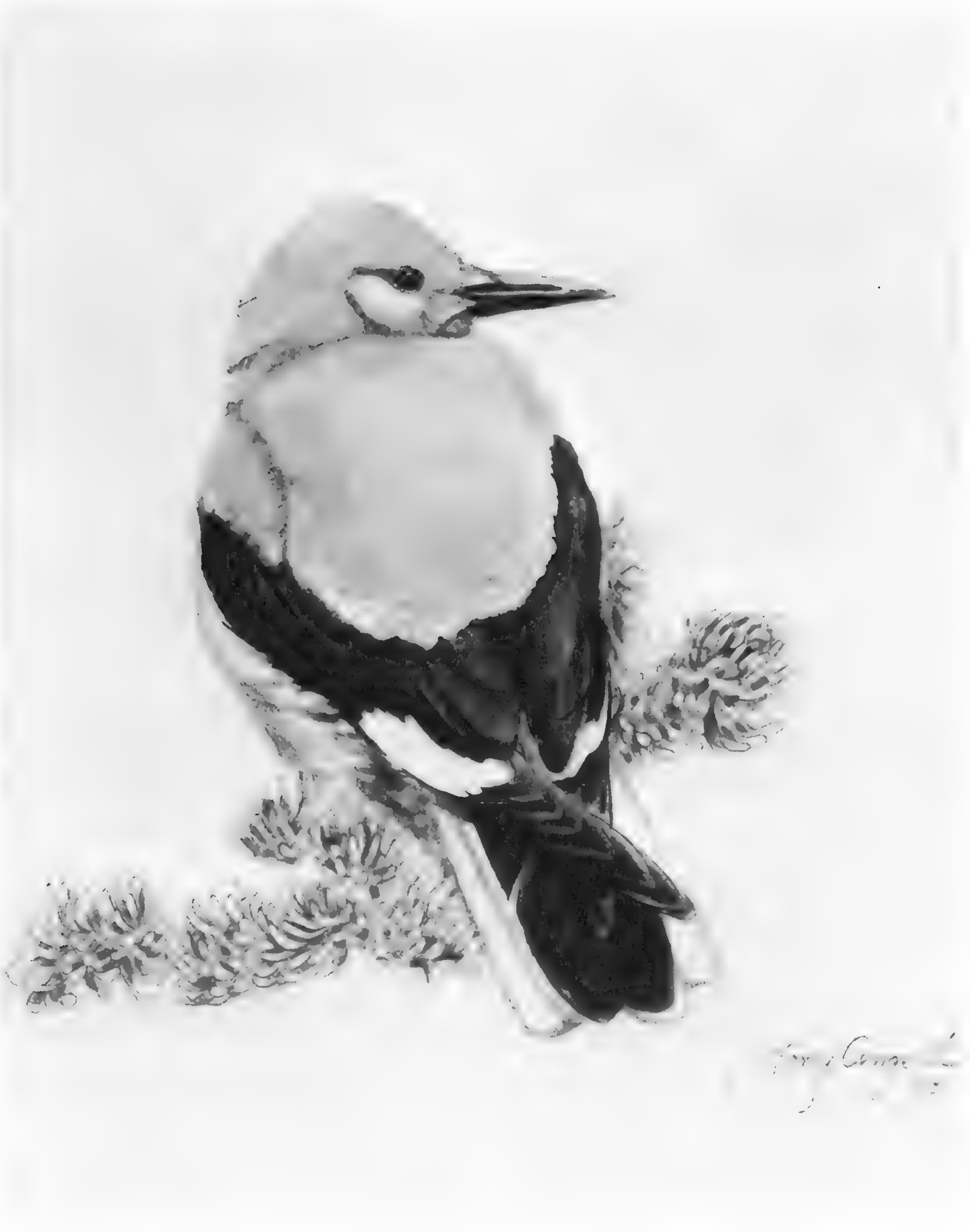

Clark's Nutcracker, *Nucifraga columbiana*. Drawing by Tony Angell.

# THE GREEN-BARRED FLICKER AND GOLDEN-GREEN WOODPECKER OF SOUTH AMERICA

Lester L. Short

The woodpeckers of the world number about 210 species, distributed throughout wooded and semi-wooded parts of every continent except Australia and Antarctica, and occurring on all large islands except Greenland, New Guinea, New Zealand, and Madagascar. I have seen 115 of these woodpeckers (representing all genera except Cuban *Xiphidiopicus*) in the field in both the New World and the Old. With 79 species, South America boasts more members of the family Picidae than any other continent, and only there and in southeastern Asia may as many as 12 or 13 species of woodpeckers coexist sympatrically. I have provided below a brief review of the natural history of two woodpeckers, the Green-barred Flicker and Golden-green Woodpecker, inimitably portrayed here by Don Eckelberry, who painted these woodpeckers in Argentina. The information about these woodpeckers is taken from my preliminary write-ups of these species for a forthcoming book treating the world's woodpeckers.

## Green-barred Flicker

The Green-barred Flicker *(Colaptes melanochloros,* formerly known as *Chrysoptilus melanochloros* and *C. melanolaimus*) is somewhat less terrestrial than are most forms of the familiar Common Flicker (*Colaptes auratus*) of North America, but its habits and vocalizations are very similar. It forms a superspecies with the Spot-breasted Flicker (*C. punctigula*) of Amazonia north to Panama. The variable Green-barred Flicker is restricted to South America, through which it ranges widely. It can be found in the arid upland valleys of Bolivia, the hilly woods and lowland savannas of Mato Grosso and other states of Brazil fringing Amazonia, on Marajo Island at the mouth of the Amazon, and in the area east of the Andes southward through forests, savannas, scrub woodlands, such as the caatinga and the chaco, and the wooded parts of the pampas to the northern edge of Patagonia. Within this vast area are several morphologically distinct, but freely interbreeding, populations. The longer tailed and greener forest-dwelling form of Brazil and adjacent Argentina and Paraguay leads a completely arboreal, ant-foraging existence like that of related species of *Piculus.* It is green above and below, with dusky wing-feather shafts, and buffy olive ear coverts. The shorter tailed and browner backed southern and western populations, on the other hand, are partly terrestrial. They have clear yellow shafts to the wing feathers, whiter underparts and ear coverts, and usually a golden patch on the breast. Worn-plumaged birds of this group are very black about the face and throat. Size variation is great, from small savanna-dwelling birds of the northeast, to birds the size of northern Common Flickers at the fringe of Patagonia. In all populations the sexes are distinguished by their "mustaches," mixed red and black in males, and black or black-and-white checked in females. Green-barred Flickers of the open country show some brownish coloration, and even flash a white rump, visible in flight. Other details concerning the distribution, intraspecific hybridization, systematics, and behavior of the Green-barred Flicker are presented elsewhere (Short, Bull. Amer. Mus. Nat. Hist., 149:1–110, 1972).

The forest form of the Green-barred Flicker gleans and probes almost exclusively for ants along the bark of trees and especially bamboos. These forest-dwelling flickers have not been seen on the ground, but rarely they may forage there. Occasionally, they peck open ant-excavated branches at various heights in trees, from which ants are "tongued" out in much the same manner of related woodpeckers of the genera *Piculus* and *Celeus*.

Non-forest forms of the Green-barred Flicker dwell in woodlands bordering grasslands or cultivated fields and forage in trees in the same way as the forest-inhabiting form. In addition, these Green-barred Flickers frequent ant nests on the ground, hopping about in the manner of the Common Flicker in North America, and in contrast to the walking gait frequently shown by its sympatric relative, the Campo Flicker (*Colaptes campestris*). In documenting the feeding association of the somewhat awkward Green-barred Flicker with the more terrestrially adapted Campo Flicker of open country in Argentina (Wilson Bull., 81:468–470, 1969), I found that one or two of the latter species sometimes foraged alongside three or four Campo Flickers on the same ant-hills. I noted these associations with sufficient frequency to speculate that the ground-feeding and less wary Green-barred Flickers to some extent may avoid predators by foraging alongside the more wary and better ground-adapted Campo Flicker.

The stomachs of 40 Green-barred Flickers, including forest and savanna forms as well as their hybrids, contained eggs, larvae, pupae, and adult soldier and worker ants of various species, including some of the genera *Crematogaster, Camponotus,* and *Paracryptocerus* (*fide* William Brown). The only stomach with food items other than ants contained fragments of two spiders mixed with ants. The esophagus of the flickers, especially of nesting adult birds, often was crammed with ants, which presumably were fed to young flickers by regurgitation.

These South American flickers nest in trees, or, where trees are scarce, in cacti and even telegraph poles. Pairs are territorial, the sexes attacking intruders sex-for-sex in the typical woodpecker manner. Green-barred Flickers, although wary, habituate well when not disturbed by humans, and I have seen nests beside the front door of houses in Argentina. The excavation of the nesting cavity occurs early in the breeding season, which in Argentina commences in September and extends until January. Commonly, three or four eggs are laid. Both parents feed ants to the hatchlings in the nest, and to the fledglings for some time after they leave the nest. The annual molt follows nesting, in the period from January to May. There is

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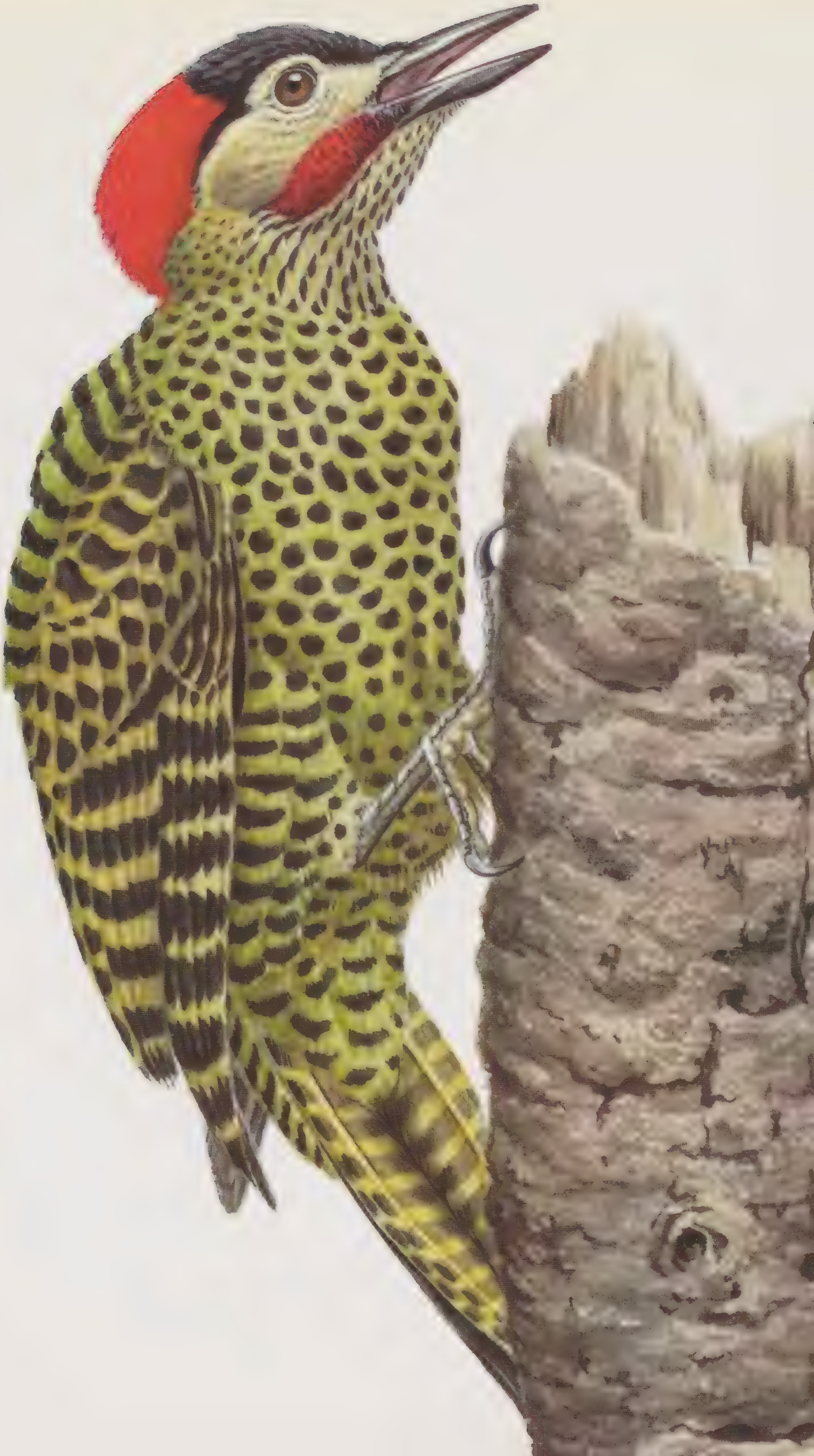
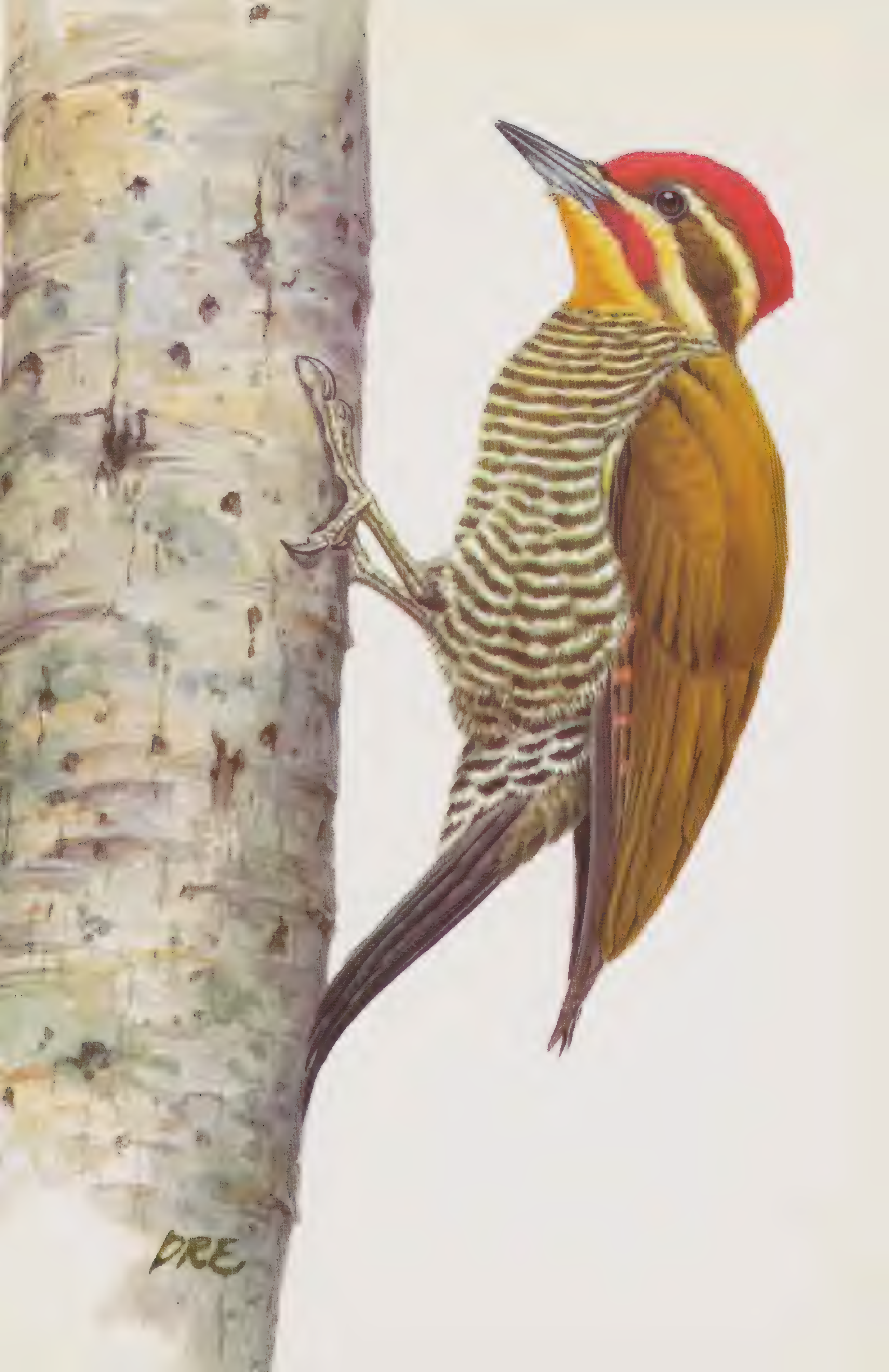
**Green-barred Flicker,** ***Colaptes melanochloros.*** **Painting by Don R. Eckelberry.**

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suggestive evidence that the southernmost populations undergo some migration northward for the winter.

The appearance and demeanor of this flicker, and its calls, are much like those of the North American flicker. The tempo of its drumming is somewhat slower than that of our North American species. An alarm Peah Call like that of the latter flicker was heard infrequently from Green-barred Flickers. The complex Wicka Call uttered by this flicker, and used in aggression and pair-formation, sounds like, and has components identical with, the Wicka Call of the North American flicker. The aggressive (territorial proclamation) Long Call, a *wick-wick-wick*—indistinguishable from some Long Calls of *Colaptes auratus*—was uttered sporadically by breeding Green-barred Flickers.

Displays of Green-barred Flickers include Swinging, Bobbing, Tail-spreading, and Wing-flicking, all of which occur also in North American flickers. Swinging involves a rhythmic, side-to-side movement of the body, and especially of the head and bill, conspicuously showing the head markings. Bobbing has a similar effect, and involves mainly the head and bill, which are moved vertically. Tail-spreading varies from a slight spreading of the feathers to a full spreading and twisting of the tail with the underside directed toward an antagonist, showing the partially yellow under-tail surface. Wing-flicking briefly reveals the yellow undersurface of the wings. All are aggressive displays, with possible pair-formation and alarm (Wing-flicking) functions, as indicated by some observations. A Wicka Call accompanied Swinging and Tail-spreading in an encounter between a male and female Green-barred Flicker in Corrientes, Argentina. Bobbing occurred not only in aggressive situations, but also when members of a pair were near one another, particularly at the time of their meeting. A male flicked its wings after supplanting its mate near a nest. Other aspects of the behavior of this attractive woodpecker remain to be studied.

## The Golden-green Woodpecker

The widespread, essentially South American Golden-green Woodpecker (*Piculus chrysochloros*) is a variable species of rather small size, weighing from 55 to 91 grams, depending upon the subspecies involved. It represents another ant-eating woodpecker group, *Piculus*, closely allied to flickers (*Colaptes*). From eastern Panama, the Golden-green Woodpecker ranges to Colombia, and southward east of the Andes to Rio de Janeiro, to Paraguay, and to the chaco of Santa Fe and Santiago del Estero Provinces in north-central Argentina. The closely related White-browed Woodpecker (*Piculus aurulentus*) of southeastern Brazil, eastern Paraguay, and Misiones, Argentina, forms a superspecies with the Golden-green Woodpecker. As the name implies, the White-browed differs from the Golden-green in having a white stripe over the eye, and it is distinguished also by its less yellowish underparts, barring beneath its wings, and red "mustaches" in both sexes. *Unmarked* cinnamon patches under the wings of the Golden-green Woodpecker are visible at close range as the bird flies. Unlike most woodpeckers, there is marked geographic variation in the sexual markings of Golden-green Woodpeckers, although males generally can be distinguished from females by their red crown and mustache patches. The behavior and interactions of forms with different sexual markings would be most interesting to study.

White-browed Woodpecker, *Piculus aurulentus*. Painting by Don R. Eckelberry.

There is extensive geographic size variation; interestingly, Amazonian and Guianan forms are larger, and birds from both north and south of those regions are smaller. Also, there appears to be geographic variation in eye color, some races having dark eyes, whereas others have white irises (Short, Amer. Mus. Novitates No. 2413, 1970).

Despite its wide range, this picid is little known. It calls infrequently and taps only sporadically, and thus is relatively inconspicuous. Forest edges, wooded savannas, and woodlands, including scrub woodland such as the Gran Chaco of Paraguay and northern Argentina, form its preferred habitat.

The Golden-green Woodpecker forages entirely on the trunk and major branches of trees, with ants forming most of its diet, although hymenopterous insects reportedly have been taken. The several stomachs I examined contained only ants. It gleans ants from tree surfaces, or from chambers within branches and branchlets, which it lays open by a short burst of taps. The ants, ant eggs, larvae, and pupae then are "tongued" up. A woodpecker may feed in one position in this manner for up to 15 minutes with little or no movement. Sometimes it moves rather slowly, foraging sporadically and pausing for long periods as do other woodpeckers. On other occasions, it moves rapidly, shifting frequently from one tree to another, gleaning and probing along the surface of the bark, but tapping only occasionally. One Golden-green Woodpecker did not tap during more than 20 minutes of active foraging.

Nesting occurs during the southern spring in Argentina. Pairs are territorial, and they are social only to the point of breakup of family groups. Holes are excavated in typical woodpecker fashion in trees, or in arboreal ant or termite nests. I discovered one nest, hollowed out of an ant or termite nest, three meters up a tree in Formosa, Argentina. A male Golden-green Woodpecker unexpectedly peered from a hole in the nest, then emerged in flight; it was joined by the female, which had been perched on the top of the ant nest. Other New World and Old World woodpeckers that also nest in ant or termite nests are species of neotropical and Asian *Celeus* (*lugubris, brachyurus*) and African *Campethera* (*nivosa*). It is not known how these woodpeckers manage to live within a swarming colony of ants. Presumably the nesting cavity is sealed over by the ants, although on some occasions the nestling woodpeckers may succumb to attacks of the ants.

It is a pity that so little is known of the behavior of this variable, fascinating woodpecker; indeed, habits of the entire genus are in need of elucidation and comparison.

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# FACTORS DIRECTING PREY-ATTACK BY THE YOUNG OF THREE PASSERINE SPECIES

Susan M. Smith

Young birds of a wide variety of species peck at an enormous range of objects, both edible and inedible. Sumner (1934), working with young hand-reared birds, reported both a Great Horned Owl (*Bubo virginianus*) and a Golden Eagle (*Aquila chrysaetos*) pecking at such objects as straws and pieces of rubber tubing. Tinbergen (1935; cited in Thorpe, 1964) wrote that young wild European Kestrels (*Falco tinnunculus*) spend hours "playing" at hunting pine cones, grass roots, etc., even after they are old enough to catch their own prey; Cade (1953) described similar behavior in a young hand-reared Gyrfalcon (*Falco rusticolus*). Nor is such behavior restricted to raptorial species. Barraud (1961) described similar behavior in several hand-reared British passerines, particularly Great Tits (*Parus major*) and Chaffinches (*Fringilla coelebs*). Horwich (1969:89) wrote that his young hand-reared Mockingbirds (*Mimus polyglottos*) directed their first pecks toward "small moving objects or small specks on the cage floor." Both Rand (1937) and Weisbrod (1970) have reported young hand-reared Blue Jays (*Cyanocitta cristata*) pecking at an incredible range of items, including rubber bands, pencils, and crayons.

Many of these and other similar reports state that pecking at inedible objects is most often seen when the birds are not hungry. Indeed, Goodwin and Hess (1969a:235) have reported of domestic chicks (*Gallus gallus*): ". . . it is possible to observe intensive pecking behavior toward inedible objects in chicks during the first two days of life, a time when the presence of yolk sac reserves makes food ingestion totally unnecessary . . ." Wolfe and Kaplon (1941) experimented with young chicks and found that the very act of pecking itself may be a kind of "reward" for this type of behavior, regardless of food intake. And Goodwin and Hess (1969a, 1969b) have demonstrated that apparently unrewarded pecking, in terms of food intake, nevertheless shows distinct and repeatable patterns that seem to reflect innate behavior related to feeding.

There have been several recent studies investigating the kinds of stimuli that elicit pecking by young birds. Many of these have used a variety of foods which the young birds are allowed to eat. The results of many of these experiments have been the interpretation of the behavior as the formation of specific search images. This concept, first proposed for wild birds by Tingergen (1960), received recent criticism (Hinde, 1970; Dawkins, 1971a); but studies like those of Allen and Clarke (1968), Croze (1970), and Mueller (1971), among others, provide strong supporting evidence for the concept of specific search images. Dawkins (1971a, 1971b) described the development of search images in domestic chicks, but related this to changes in perceptual ability of the chicks, probably caused simply by structural development of the central nervous system. Coppinger's (1970) work on young birds of three passerines showed that previous experience had a measurable effect on their feeding behavior. Rabinowitch experimented both with Ring-billed and Herring Gulls (1968) and with Zebra Finches, *Taeniopygia castanotis* (1969). In each case, he showed that young birds form definite food preferences on the basis of their early feeding experience. He also showed that there were consistent preferences, even among unfamiliar foods, shown by both the gulls and the Zebra Finches. His data, therefore, indicate some apparently innate food preferences in all three species.

Fewer studies have been done on the kinds of stimuli that elicit pecking by young birds when offered inedible objects. Goodwin and Hess (1969a) performed such an experiment with young chicks and demonstrated that the form of an object can effect its likelihood of being pecked. However, they did not report the location of the pecks on the various objects used in their experiments.

Very little has been done to determine what aspects of a potential food item actually serve to direct the location of young birds' pecks. In a previous study (Smith, 1973), I investigated this aspect of prey attack with hand-reared Loggerhead Shrikes (*Lanius ludovicianus*), passerines that regularly kill and eat small vertebrate prey. I presented the shrikes with wooden models bearing various cues such as "eyes" or a "neck." The shrikes received the entire series of models twice, the only difference in the two presentations being that the birds were older the second time. The birds responded significantly to every cue presented. However, only one cue, motion, elicited a higher response in the second presentation; by contrast, the responses to the other three cues waned. Also, there was no consistent evidence that the birds responded more strongly when more than one of the cues were given at a time (heterogeneous summation). I interpreted these results as indicating that, while the shrikes' response to motion was probably innate, their responses to the other three cues were due simply to curiosity. If this interpretation is correct, then non-predatory passerine species should show similar responses to similar cues.

The present paper describes experiments designed to test this prediction, and to investigate with hand-reared, naive young birds what aspects of a novel potential food item serve to direct their pecks. I performed the experiments with Black-capped Chickadees (*Parus atricapillus*), Gray Catbirds (*Dumetella carolinensis*), and Blue Jays (*Cyanocitta cristata*).

## *Methods*

In the summer of 1971, I hand-reared four chickadees from one brood, four catbirds from two broods, and five jays from two broods. The chickadees were approximately eleven days old when they were removed from their nest, the catbirds six to seven days old, and the jays approximately twelve days old.

I kept the young birds in cages made of hardware cloth attached to wooden frames measuring 30 × 18 × 18 inches. All four chickadees lived in one cage. Two catbirds were kept in each of two cages. The jays occupied double cages joined end to end. Two such units housed two jays each and one contained a single bird.

I fed the birds a high protein diet with vitamin and calcium supplements, giving all three species canned dogfood regularly, along with chopped fresh meat such as pork kidney or lambs heart when available. They were all initially hand-fed with forceps but later fed themselves from dishes on the floor of their cages. All the birds ate live meal-worms daily, and the catbirds also ate a variety of locally available berries.

For each species, I constructed a series of cylindrical wooden models approximately the size of the largest insect larva that these species might encounter naturally: for chickadees, 1¼ inches long by 3/16 inches in diameter; for catbirds, 1½ by 5/16 inches; for Blue Jays, 2 by ⅜ inches. Six different cues were devised: ink eyespots, black pinhead "eyes," single yellow pin "head," bristle "legs," neck constriction, and motion (see Figure 1). Models representing none, or one or more, of the clues were presented to the three species. I divided each model lengthwise into thirds by light pencil marks, simply to aid in scoring the location of the birds' pecks during the experiments. I did not see any individual of the three species directing its pecks at these faint pencil lines. Whenever more than one cue was given, the birds pecked consistently at the same third of the model. The cue was always placed on one end, recorded as the "head." I referred to the other two thirds as "middle" and "tail." Hence, in the experiments reported here, neither the middle nor the tail ever bore any cues. Of the cues presented in these experiments, four (motion, neck, and both kinds of eye) made up the entire series of cues given to the shrikes (Smith, 1973).

The simpler models were presented to the birds before the more complex ones, the first bearing no cues at all. The first models were motionless; then the same series was presented to the birds with movement of each model. Each cage had a diagonal slit in its floor and was raised so that my arm could move freely beneath it. The models to be moved each had a nail projecting from below (see Figure 1), which could be inserted through the diagonal slit and grasped from underneath. Thus, the speed and direction of the model could be modified at will, although the path was confined to a straight diagonal track. In the motion experiments the models were always oriented lengthwise along the track. I have described this method of effecting motion more fully elsewhere (Smith, 1973).

Because of the method used to create the moving models, the birds could not pick them up as they could the still models, which were not fastened down. However, the weight of the models was too great to allow any of the birds to carry them more than a few centimeters.

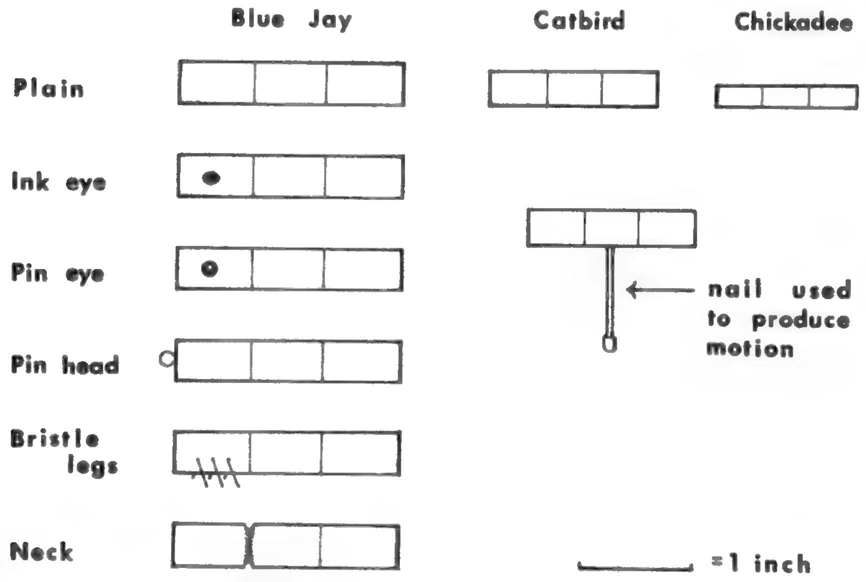

Figure 1. Kinds of models used, shown in side view. Along the top are the three sizes of models drawn to scale for each of the three species to which the models were presented. Each of the cues is shown only for the Blue Jay. See text for an explanation of how motion was achieved.

TABLE 1

Responses of Black-capped Chickadees to the Still Models

| *Model* | *Total pecks* | *Percentage of pecks at:* *Ends* | *Head* | *Middle* | *Tail* | *Significance level* ($X^2$) |
|---|---|---|---|---|---|---|
| Plain | 85 | 88.2 | — | 11.8 | — | .01 E[1] |
| Ink-eyespot | 191 | — | 44.5 | 13.1 | 42.4 | — |
| Pin-eye | 161 | — | 83.2 | 6.8 | 9.9 | .01 H[2] |
| Pin-head | 179 | — | 49.0 | 5.0 | 46.0 | — |
| Bristle-legs | 117 | — | 64.1 | 1.7 | 34.2 | .01 H |
| Pin-head + legs | 60 | — | 90.0 | — | 10.0 | .01 H |
| Neck | 130 | — | 65.4 | 0.8 | 33.8 | .01 H |
| Neck + ink-eye | 197 | — | 60.9 | 1.0 | 38.1 | .01 H |
| Neck + pin-eye | 147 | — | 91.2 | — | 8.8 | .01 H |
| Neck + pin-head | 137 | — | 83.2 | 1.5 | 15.3 | .01 H |
| Neck + legs | 14 | — | 100.0 | — | — | .01 H |
| Neck + legs + pin-head | 215 | — | 65.6 | 0.5 | 33.9 | .01 H |

[1] E indicates the ends of the model received a significantly greater percentage of pecks.

[2] H indicates the head of the model received a significantly greater percentage of pecks.

I began the experiments for each species only after all the birds were capable of catching and eating mealworms for themselves. The chickadees and catbirds were 35 days old when they received their first models; the jays were 27 days old. In a few of the earliest experiments, the birds only received one model per day, but on most days I presented the birds with one model in the morning and another in the late afternoon. Furthermore, since each moving model was presented twice (once "forward" and once "backward") the birds received four tests per day during the last days of the study. Each test lasted five minutes, during which I recorded the number of pecks given to each third of the model.

I analyzed the data in two steps, each using $X^2$ analysis. The first involved only the plain models. I made no attempt to distinguish between the two end thirds of this model during the experiments; to do so would have been impractical, as each species could pick up their models, or spin them rapidly with a strong peck. My null hypothesis for the plain models was that the species would peck evenly at all thirds of the model, i.e., the ends should have received two-thirds of the pecks. In all three species, this null hypothesis proved to be incorrect: each bird directed significantly more pecks at the two ends than the 66.7 per cent predicted. I then used this finding in the second step of the analysis. For all the other models, pecks to the middle third were ignored, and I hypothesized that there would be an equal number of pecks directed toward each of the two ends, regardless of the presence of any cues.

## *Responses to the Still Models*

Tables 1, 2, and 3 give the responses of the three species to their series of still models. In general, all three species showed definite responses to the cues tested. Indeed, the chickadees were the only ones that did not give a significant response to every cue-bearing model. They responded significantly to nine of the 11 models given. And even in the two models where no statistically significant responses were elicited, the chickadees pecked slightly more at the cue-bearing third than at the tail (Table 1).

Certain cues seemed to be considerably more attractive to the birds than others. This is particularly noticeable when one compares the responses of all three species to the two kinds of eyes: every species gave a higher response to the pinhead-eye than to the ink-eye. The bristle-legs also appeared to be especially attractive to the catbirds and the jays.

However, none of the three species showed any consistent evidence of heterogeneous summation when two or more cues were given simultaneously. For example, the chickadees gave a 100 per cent response to the head of the model bearing neck plus legs, but only a 65.6 per cent response to the head of the model bearing neck plus legs plus pin-head (Table 1). Similarly, the catbirds gave a 96.4 per cent response to the head of the model bearing neck plus legs, but only an 86.2 per cent response to the head of the model bearing neck plus legs plus pin-head (Table 2). Finally, the jays gave a 79.9 per cent response to the model bearing the ink-eyespot, but only a 74.7 per cent response to the head of the model bearing both an ink-eyespot and a neck-constriction (Table 3).

## *Responses to the Moving Models*

The responses of the three species to the moving models are given in Tables 4, 5, and 6. The chickadees responded only to the first three moving

TABLE 2

Responses of Catbirds to the Still Models

| | | *Percentage of pecks at:* | | | | |
|---|---|---|---|---|---|---|
| *Model* | *Total pecks* | *Ends* | *Head* | *Middle* | *Tail* | *Significance level* ($X^2$) |
| Plain | 492 | 79.0 | — | 21.0 | — | .01 E[1] |
| Ink-eyespot | 482 | — | 68.6 | 12.7 | 18.7 | .01 H[2] |
| Pin-eye | 186 | — | 81.0 | 4.4 | 14.6 | .01 H |
| Pin-head | 201 | — | 71.0 | 3.9 | 25.1 | .01 H |
| Bristle-legs | 47 | — | 85.0 | 15.0 | — | .01 H |
| Pin-head + legs | 199 | — | 82.9 | 1.2 | 15.9 | .01 H |
| Neck | 111 | — | 62.6 | 18.7 | 18.7 | .01 H |
| Neck + ink-eye | 92 | — | 67.4 | 21.7 | 10.9 | .01 H |
| Neck + pin-eye | 80 | — | 86.7 | 0.8 | 12.5 | .01 H |
| Neck + pin-head | 167 | — | 58.9 | 7.6 | 33.5 | .05 H |
| Neck + legs | 85 | — | 96.4 | 0.7 | 2.9 | .01 H |
| Neck + legs + pin-head | 161 | — | 86.2 | 0.6 | 13.2 | .01 H |

[1] E indicates the ends of the model received a significantly greater percentage of pecks.

[2] H indicates the head of the model received a significantly greater percentage of pecks.

models. After that, beyond a brief glance at the beginning of the experiment, all the chickadees ignored the rest of the models completely.

The first moving model presented to each species was plain, with no cue except motion. All three species were apparently somewhat frightened by their first moving models, as evidenced by their sleeked plumage and wagging tails; nevertheless, even the chickadees appeared highly interested in these first ones. When the model moved toward a bird, the bird often backed away and watched until the model had gone by. When the model had passed the bird and it appeared to retreat, the bird usually followed it. This may explain why the two smaller species (chickadees and catbirds) gave statistically significant responses to the trailing third of the plain moving model. The jays also pecked more at the trailing third, although their response was not statistically significant.

All other moving models bore additional cues. From then on, with only one exception (jays' model with the ink-eyespot moving backward), the birds responded more frequently toward the cue-bearing third, regardless of whether it was leading or trailing. Indeed, both catbirds and jays, when presented with the same model moving forward (F), then backward (B), showed a greater response to the cue-bearing third when it was trailing than when it was leading (Tables 5 and 6). Motion itself, therefore, does not direct the pecks of either catbirds or jays to the leading, or head, end of potential prey; furthermore, the direction of movement is easily overridden by the presence of even the weakest of the other cues tested.

All of the cues presented in the still models were also given in the moving models. Again, neither the catbirds nor the jays gave any consistent

## TABLE 3

Responses of Blue Jays to the Still Models

| *Model* | *Total pecks* | *Percentage of pecks at:* | | | | *Significance level* ($X^2$) |
|---|---|---|---|---|---|---|
| | | *Ends* | *Head* | *Middle* | *Tail* | |
| Plain | 265 | 93.6 | — | 6.4 | — | .01 E[1] |
| Ink-eyespot | 309 | — | 79.9 | 2.3 | 17.8 | .01 H[2] |
| Pin-eye | 566 | — | 86.9 | 3.9 | 9.2 | .01 H |
| Pin-head | 403 | — | 85.6 | 3.2 | 11.2 | .01 H |
| Bristle-legs | 315 | — | 80.0 | 3.2 | 16.8 | .01 H |
| Neck | 330 | — | 60.3 | 7.0 | 32.7 | .01 H |
| Neck + ink-eye | 296 | — | 74.7 | 2.0 | 23.3 | .01 H |
| Neck + pin-eye | 346 | — | 87.3 | 2.3 | 10.4 | .01 H |
| Neck + pin-eye + legs + pin-head | 305 | — | 93.4 | 2.0 | 4.6 | .01 H |

[1] E indicates the ends of the model received a significantly greater percentage of pecks.

[2] H indicates the head of the model received a significantly greater percentage of pecks.

TABLE 4

Responses of Black-capped Chickadees to the Moving Models

| *Model* | *Total pecks* | *Percentage of pecks at:* Head | Middle | Tail | *Significance level* ($X^2$) |
|---|---|---|---|---|---|
| Plain | 81 | 33.3 | 1.2 | 65.5 | .01 T[1] |
| Ink-eye (F)[2] | 38 | 81.6 | 2.6 | 15.8 | .01 L[3] |
| Pin-eye (F) | 13 | 76.9 | — | 23.1 | — |

[1] T indicates the response was significant to the trailing end.

[2] (F) indicates model was moved forward with the cue-bearing end first.

[3] L indicates the response was significant to the leading end.

evidence of heterogeneous summation when more than one cue was present. For example, the catbirds' response to the cue-bearing third of the model having neck plus legs was 79.3 per cent (F) and 75.0 per cent (B); while their response to the cue-bearing third of the model having neck plus legs plus pin-head was 50.0 per cent (F) and 66.9 per cent (B) (Table 5). Similarly, the jays' response to the cue-bearing third of the model bearing pin-eye alone was 80.4 per cent (F) and 73.0 per cent (B); while their response to the cue-bearing third of the model having neck plus pin-eye plus legs plus pin-head was 66.2 per cent (F) and 85.1 per cent (B) (Table 6).

## *Discussion*

The basic question underlying these experiments is: how do young birds become able to recognize, react to, and successfully capture their own food? Even in species with highly dependent altricial young, this ability in most cases is probably not "taught" by the adults. Wortis (1969) described an interesting situation in the Ring Dove (*Streptopelia risoria*), whose altricial young apparently require normal social interactions with their parents in order to begin pecking at grain themselves. However, this dependence appears to be unusual. Certainly, hand-reared birds of a wide variety of species can develop adult patterns of prey-attack in the absence of parent birds. This includes even predatory passerines like Loggerhead Shrikes, in which this behavior is highly complex (Smith, 1973). Some combination of curiosity, innate behavior, and learning by experience is probably responsible for the development of food recognition and attack in most species. It is difficult to distinguish between innate and learned behavior in this context (see, for example, Hailman, 1969). Nevertheless, certain behaviors appear to be elicited in inexperienced birds in apparently species-specific patterns, although the recent work of Coppinger (1970) stresses the danger of generalizing too freely, even among so-called "naive" birds.

In the data from the present experiments, the responses of all three species to the moving models bear comparison with the responses of young shrikes to the same stimulus. Thus, to the chickadees, catbirds, and jays, motion itself was clearly not a highly directing cue. When it was presented in combination with any other cue, all three species nearly always gave statistically significant responses to the end bearing the other cue(s), regardless of whether this was leading or trailing. In the plain moving model, both the chickadees and the catbirds gave a significant response to the trailing third, and the jays, whose pecks were far more evenly distributed, also pecked more at the trailing third. This is in sharp contrast to the behavior of the Loggerhead Shrikes, whose responses to all moving models, including the plain one, were highly directed to the leading third of the model. Presumably the shrikes' response to motion is adaptive to their predatory mode of life. It allows them to react to rapidly-moving and potentially dangerous prey, such as mice, by directing their pecks to the back of the neck. Black-capped Chickadees, Gray Catbirds, and Blue Jays normally do not capture prey large and agile enough to escape or defend

TABLE 5

Responses of Catbirds to the Moving Models

| *Model* | *Total pecks* | *Percentage of pecks at:* *Head* | *Middle* | *Tail* | *Significance level* ($X^2$) |
|---|---|---|---|---|---|
| Plain | 79 | 10.3 | 12.5 | 77.2 | .01 T[1] |
| Ink-eye (F)[2] | 115 | 60.9 | 1.7 | 31.4 | .05 L[3] |
| Ink-eye (B)[4] | 178 | 15.7 | 5.2 | 79.1 | .01 T |
| Bristle-legs (F) | 197 | 67.0 | 3.0 | 30.0 | .01 L |
| Bristle-legs (B) | 143 | 16.1 | — | 83.9 | .01 T |
| Neck (F) | 182 | 50.5 | 3.2 | 46.2 | — |
| Neck (B) | 113 | 24.8 | 7.1 | 68.1 | .01 T |
| Neck + ink-eye (F) | 67 | 70.1 | 6.0 | 23.9 | .01 L |
| Neck + ink-eye (B) | 122 | 31.1 | 3.3 | 65.6 | .01 T |
| Neck + pin-eye (F) | 83 | 67.5 | 3.6 | 28.9 | .01 L |
| Neck + pin-eye (B) | 44 | 47.7 | 2.3 | 50.0 | — |
| Neck + pin-head (F) | 132 | 50.8 | 7.5 | 41.7 | — |
| Neck + pin-head (B) | 136 | 36.8 | 6.6 | 56.6 | .05 T |
| Neck + legs (F) | 150 | 79.3 | 8.7 | 12.0 | .01 L |
| Neck + legs (B) | 124 | 23.4 | 1.6 | 75.0 | .01 T |
| Neck + legs + pin-head (F) | 182 | 50.0 | 4.9 | 45.1 | — |
| Neck + legs + pin head (B) | 133 | 27.1 | 6.0 | 66.9 | .01 T |

[1] T indicates the response was significant to the trailing end.
[2] (F) indicates model was moved forward with the cue-bearing end first.
[3] L indicates the response was significant to the leading end.
[4] (B) indicates the model was moved backward with the cue-bearing end last.

itself if not killed instantly; therefore, specialized inborn recognition of the vulnerable "back of neck" through direction of movement is not a necessary adaptation in these species.

It might be argued that the degree to which the birds could manipulate the models might have had an effect on their responses to the models. All the moving models were necessarily held down by the nail used to make them move, whereas the birds could pick up and move the still models. As pointed out above, the weight of the models prevented their being carried any distance. It could even be postulated that the opportunity to chase after an object that is retreating, such as was provided by the moving models, would balance any added reinforcement caused by the extra degree of manipulation provided by the still models. In any case, the effect of reinforcement in experiments of this kind is not easily measured.

## TABLE 6

### Responses of Blue Jays to the Moving Models

| *Model* | *Total pecks* | *Percentage of pecks at:* | | | *Significance level* ($X^2$) |
|---|---|---|---|---|---|
| | | *Head* | *Middle* | *Tail* | |
| Plain | 138 | 48.5 | 2.2 | 49.3 | — |
| Ink-eye (F)[1] | 122 | 88.5 | — | 11.5 | .01 L[2] |
| Ink-eye (B)[3] | 36 | 52.8 | — | 47.2 | — |
| Pin-eye (F) | 143 | 80.4 | 0.7 | 18.9 | .01 L |
| Pin-eye (B) | 74 | 25.7 | 1.3 | 73.0 | .01 T[4] |
| Pin-head (F) | 171 | 84.2 | 1.8 | 14.0 | .01 L |
| Pin-head (B) | 124 | 16.9 | 1.6 | 81.5 | .01 T |
| Bristle-legs (F) | 75 | 64.0 | 1.3 | 34.7 | .05 L |
| Bristle-legs (B) | 124 | 16.1 | — | 83.9 | .01 T |
| Neck (F) | 57 | 52.6 | 3.5 | 43.9 | — |
| Neck (B) | 37 | 37.8 | — | 62.2 | — |
| Neck + ink-eye (F) | 73 | 75.4 | 2.7 | 21.9 | .01 L |
| Neck + ink-eye (B) | 38 | 15.8 | 5.3 | 78.9 | .01 T |
| Neck + pin-eye (F) | 38 | 60.5 | 2.6 | 36.9 | — |
| Neck + pin-eye (B) | 135 | 20.0 | 2.2 | 77.8 | .01 T |
| Neck + pin-eye + legs + pin-head (F) | 136 | 66.2 | 4.4 | 29.4 | .01 L |
| Neck + pin-eye + legs + pin-head (B) | 67 | 14.9 | — | 85.1 | .01 T |

[1] (F) indicates model was moved forward with the cue-bearing end first.

[2] L indicates the response was significant tot he leading end.

[3] (B) indicates the model was moved backward with the cue-bearing end last.

[4] T indicates the response was significant to the trailing end.

Mueller (in press) carried out model experiments with several hand-reared American Kestrels (*Falco sparverius*). One of his models was a tissue paper "mouse," complete with red cotton eyes and string tail. A model "mouse" contained about one gram of mouse flesh, and any bird attacking the model sufficiently to find the concealed meat was allowed to eat it. The only hawk that succeeded in finding the meat attacked the model in eight of 12 presentations. It found and ate the meat in the fifth and sixth attacks, but in the next two attacks did not tear up the model sufficiently to find the meat. Apparently, for this particular bird at least, any reinforcement provided by the meat was not strongly important in its response to the paper "mouse."

Turning to the still models in the present experiments, the responses of each species to the models bearing the pin-eyes seem to suggest a possible inborn response to this cue. All three species directed more than 80 per cent of their pecks to the head of the model bearing the pin-eyes alone; both the chickadees and the jays gave higher responses to the pin-eye than to any other single cue, and the catbirds responded more strongly to only one other cue presented singly (bristle legs). Moreover, in every species, the response to a combination of the pin-eyes and one other cue was greater than the responses to either of the cues singly (Tables 1, 2, and 3).

All three species gave much stronger responses to the pin-eyes than to the flat ink-eyespots. This difference cannot be explained solely by the difference in shininess and texture, as in all three species the pin-eyes elicited greater responses than did the pin-head.

The responses to the pin-eyes are particularly interesting in light of the experiments published by Blest (1957). He showed that small round spots found on certain butterflies' wings, and perhaps resembling eyes, do in fact draw the pecks of adult insectivorous birds away from the body of the butterflies to their less vulnerable wings. He also did experiments offering mealworms, some of which had been painted with a single dark eyespot at one end, to four hand-reared inexperienced Yellowhammers (*Emberiza citrinella*). All gave significant responses to the spotted end. Blest felt that this attraction toward small round spots, shown by Great Tits and Chaffinches as well as Yellowhammers, might be a general characteristic of many insectivorous birds.

The present data might be interpreted as supporting Blest's hypothesis, and as suggesting that the mechanism requires no experience by the birds, since their only live food throughout this study was mealworms, which normally do not possess any obvious eyespots. Nevertheless, while the responses of all three species to the still models bearing pin-eyes are highly suggestive, the responses to the moving models with pin-eyes do not conform to the pattern. Still, the fact that there is some evidence of summation with this cue in all three species requires some explanation. Further experiments should be done to explore this possibility.

There is no evidence of any inborn response to any of the other cues presented to the three species. The lack of any consistent summation of response among these cues is particularly revealing. All three species tended to give a fairly uniform response to the different end, regardless of how many cues were available to mark it as being different. These data suggest that curiosity, itself, may play a highly significant role in the development of feeding behavior in these young birds.

Vince (1960) did one of the few studies on levels of curiosity in young passerines. Working with the pecking response to small, brightly colored objects, she demonstrated that young Great Tits showed a definite peak of interest between ten and fifteen weeks after fledging. Their response level then waned considerably, and, by the age of thirty weeks, had reached the level shown by adults.

The whole role of curiosity and novelty in the development of feeding behavior in birds presents some interesting problems. Coppinger (1969, 1970) has data for several passerine species, which he interprets as showing that, in some cases at least, even young birds avoid novelty. Similarly, Shettleworth (1972) showed that domestic chicks more readily learn to reject bad-tasting water if the noxious stimulus is also novel in some aspect such as color, while the good-tasting water is a familiar color. On the other hand, there are in the literature many reports, some of which are mentioned above, of young birds pecking at strange objects. Nor is this confined to juvenile birds; Mueller (1971) has shown that for both American Kestrels and Broad-winged Hawks (*Buteo platypterus*), "oddity" is very nearly as important as specific search image in eliciting attack.

None of the three species in the present study showed any sign of rejecting novelty *per se* in their responses to the models. They eagerly attacked all still models and at least the first moving ones. Only the chickadees rejected any models — every model after the first three moving ones. This rejection definitely was not due to novelty, as the chickadees had already responded both to motion itself and to all the other cues on the still models. This rejection, in fact, is probably best explained in terms of waning levels of curiosity in these birds.

The three species used in this study are essentially omnivorous (Bent, 1946, 1948). It seems unlikely that such birds would possess the precise innate recognition of prey such as has been demonstrated in various predatory species (e.g., Smith, 1973; Mueller, in press). Indeed, considering both the wide variety of food eaten by members of a local population of any of these three species and the geographical variation within their ranges, such innate recognition of any particular food type would seem to convey little selective advantage to these species.

Possibly every bird, regardless of its natural diet, experiences a conflict between couriosity and rejection of novelty. The balance of these two factors probably varies with the age of the individual. It almost certainly will also vary from species to species. Those species with the most varied or least predictable food supplies will probably have a very different balance between novelty and curiosity from those with highly stable, predictable diets. Comparative studies with both adults and juveniles of such species should help elucidate the relative roles of curiosity and rejection of novelty in the development of their food recognition and attack.

## *Summary*

Experiments designed to investigate what aspects of a potential food item are used by young inexperienced birds to direct their attack were performed with hand-reared young Black-capped Chickadees, Gray Catbirds, and Blue Jays. The birds were tested with wooden models to which six cues in various combinations could be added: ink eyespots, black pinhead eyes,

single yellow pin "head," bristle "legs," neck constriction, and motion. Of these, one cue, motion, clearly was not a directing stimulus to any of the three species. All of the birds responded strongly to the other five cues. I suggest that their responses to at least four of these were due to curiosity. Further experiments should be done to find if the response to black pinhead eyes, or pin-eyes, might actually be inborn in any of the three species. The relative roles of curiosity and various other factors in development of food recognition and attack are discussed with respect to the natural diet of the birds studied.

## *Acknowledgments*

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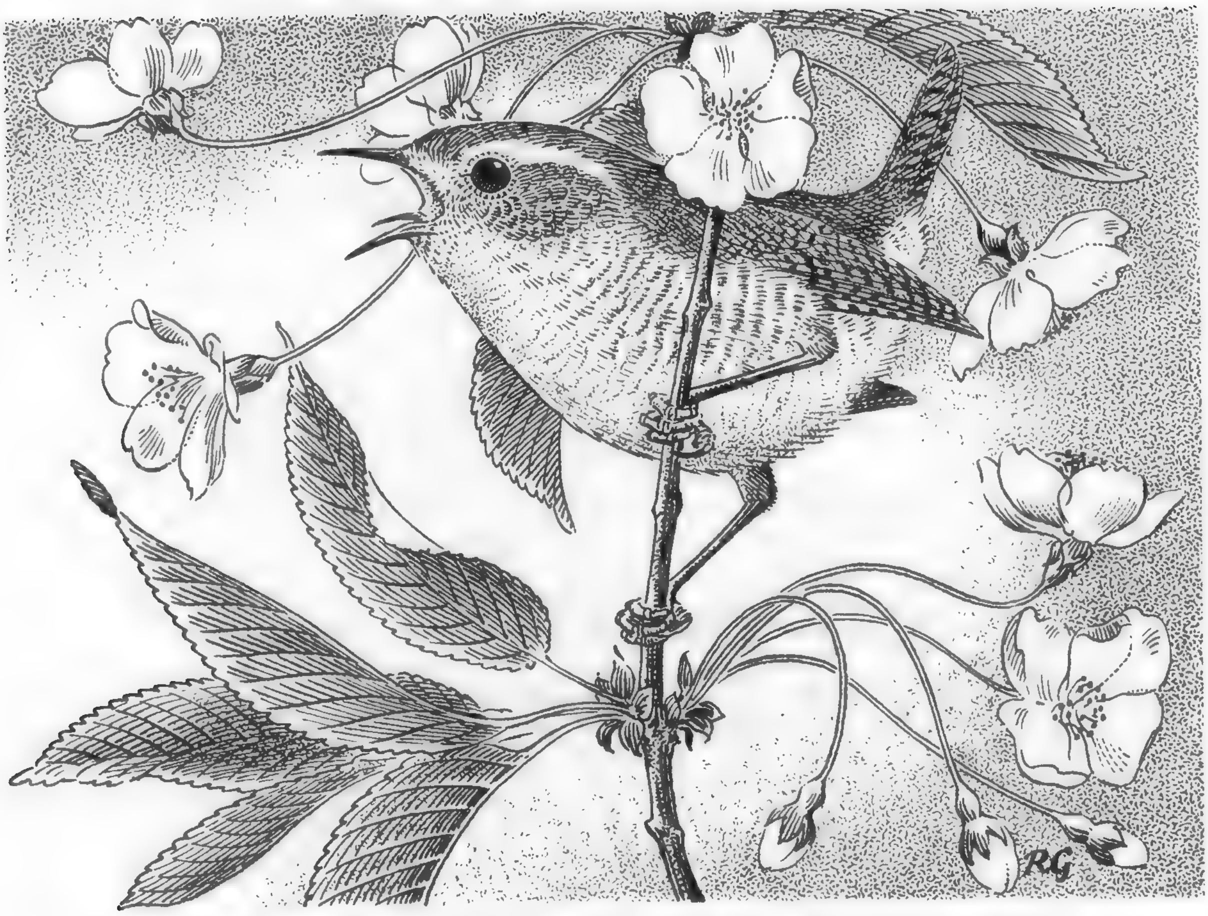

Winter Wren, *Troglodytes troglodytes*. Drawing by Robert Gillmor.

# ADAPTIVE ASPECTS OF THE MOUNTAIN PLOVER SOCIAL SYSTEM

Walter D. Graul

Photographs and black-and-white drawings by the author

Research on avian behavior has been greatly stimulated in recent years by studies showing that ecology of species determines the nature of many aspects of behavior, including overall social organization (Crook, 1964, 1965; Cullen, 1957; Orians, 1961, 1969; Verner and Willson, 1966).

The results of studies of behavioral adaptations among shorebirds show that this group (suborder Charadrii) is characterized by a wide variety of social systems. Many species are monogamous (Holmes, 1966, 1973; Holmes and Pitelka, 1964; Lack, 1968); some are apparently polygynous (Pitelka, 1959); others are polyandrous (Hays, 1972; Jenni and Collier, 1972; Raner, 1972; Oring and Knudson, 1972; Pulliainen, 1970); a few have lek systems (Hogan-Warburg, 1966); and still others have social systems in which females lay one clutch for a male to incubate and then a second clutch which they incubate themselves (Hildén, 1965; Parmelee, 1970; Parmelee and Payne, 1973). The present study of the Mountain Plover (*Charadrius montanus*) is a contribution to this area of study. All previously existing information on the breeding behavior of this species comes from a single study (Laun, 1957), except for a few anecdotal reports.

## *Breeding Range and Study Area*

The Mountain Plover breeds in the shortgrass prairie on the arid, high plains east of the Rocky Mountains in the central United States. Bailey and Niedrach (1965) record the breeding range from New Mexico into Canada, extending eastward as far as western North Dakota and Oklahoma. Laun (1957) failed to find evidence, through extensive correspondence, of recent nesting in North Dakota, South Dakota, Nebraska, and Kansas.

In an attempt to further understand the present breeding range of this species, I corresponded extensively and traveled through many areas where it supposedly breeds. My findings support Laun's contention that it does not breed in the four states of the Great Plains mentioned above. Small populations still breed in parts of Montana, Wyoming, Oklahoma, and New Mexico, but northeastern Colorado appears to be the present stronghold of this species.

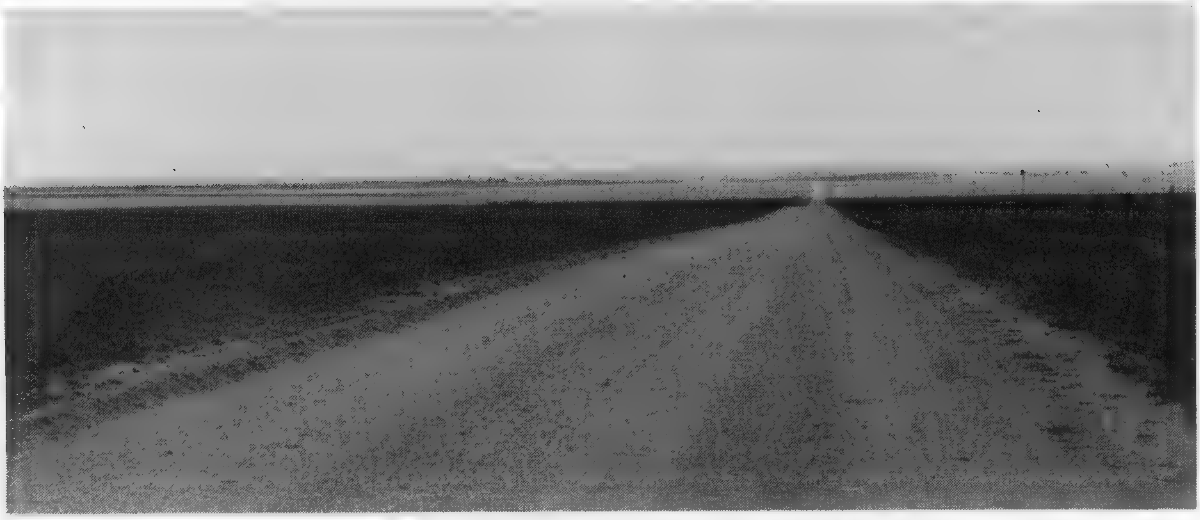

Figure 1. View of a road transecting the main study area near Keota, Colorado. Mountain Plovers nest throughout this region.

Therefore, I selected two study areas in northern Weld County in northeastern Colorado. The major study area, on the Pawnee National Grassland, consisted of 16 square kilometers just southwest of Keota. I established a secondary study area on the International Biological Program's Pawnee Site, approximately 64 km northwest of the main study area. Additionally, I observed small populations at scattered locations on the Pawnee National Grassland between these two areas.

This general area is part of the high shortgrass prairie (elevation about 1,470 meters) and consists of gently rolling hills with extensive flats, playas, and intermittent streams (Figure 1). Here, Mountain Plovers are restricted essentially to breeding in flat, heavily grazed areas (Figure 2), where the dominant vegetation includes blue grama grass (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), with western wheat grass (*Agropyron smithii*), fourwing saltbush (*Atriplex canescens*), and prickly pear cactus (*Opuntia polycantha*) also present.

The climate of the area during the breeding season is hot and dry. The average yearly precipitation ranges from 30 to 38 centimeters throughout the region, but precipitation is unevenly distributed on a year, seasonal, and area-to-area basis (Badaracco, 1971). For Grover (24 kms north of Keota), the average maximum temperatures are April, 16° C; May, 21° C; June, 27.2° C; July, 30° C; August, 32.2° C. The averages, however, obscure the fact that the daytime temperature commonly reaches 37.7° C (100° F) in June, July, and August.

## *Methods*

I spent the following periods on the study areas in northeastern Colorado: 18 March through 15 August 1969; 25 May through 29 May 1970; 1 June through 31 July 1971; 31 March through 19 May 1972.

I maintained dawn to dusk observations throughout most of the study and supplemented these with night observations. I made most of my observations from a car using a 15 to 60× spotting scope.

I marked thirty-seven adults, captured at the nest or with broods, with combinations of colored leg bands and numbered aluminum bands. In 1972, six additional adults were marked by placing "Thief Detection Powder" (Faurot, Inc., 299 Broadway, New York, New York 10007) in the nest cup. I located a total of 133 nests and an additional 60 broods during the study and placed colored and aluminum leg bands on 229 chicks associated with these nests and broods. All positive identifications of sex were obtained either by collecting the birds or by observing copulating adults.

## *Establishment of Territory*

In the spring I first saw Mountain Plovers near Keota on 22 March in 1969 and on 21 March in 1972. Early flocks contain up to 10 individuals, but groups of three to six are more common. Both courtship and copulations occur in the early flocks. Birds in such flocks are aggressive and most individuals maintain an individual distance of about 6 to 15 m. Within a few days these early flocks disperse over the breeding ground.

### Fidelity to Nesting Areas

At least some adults of both sexes return to the same area each year. Of eight adults banded at nests on a 65-hectare area in 1969, five were found the following year on nests in the same area. Four of the returns were males that sat on nests within 100 m of their 1969 nests, and the fifth return was a female that nested 340 m from her 1969 nest. In 1972, I located seven birds that had been banded at nests in 1971. Of these, two females and one

Figure 2. Prime nesting habitat of the Mountain Plover, which prefers to nest on the broad flat expanses shown here. Blue-grama grass and buffalo grass predominate as cover, with scattered patches of western wheat grass and scattered prickly pear cactus also present.

male were on nests within 100 m of their 1971 nests. Another female incubated 250 m from her 1971 nest, and one female and one male sat on nests 800 m from their 1970 nests.

At least some chicks also return to breed in the area where they hatched. One female, banded as a chick in 1969, nested in 1972 within 100 m from where she hatched. And a male, banded as a chick in 1971, nested in 1972 eight km from where he hatched.

Males commonly reoccupy their old territories, which they defend against other males. Five of six males (83%) were on nests within 100 m of their nesting sites of previous years, while only two of five females (40%) were on nests within 100 m of where they nested in previous years. Although females also frequently return to the same area each year, at least some apparently visit the territories of several males before selecting mates.

Even before females select a mate they try to chase out other females that they encounter; thus, males initially react aggressively toward males, and females toward females.

Data on the size of territories are limited. My detailed observations in 1972 indicated that three marked males defended areas of about 16 hectares each, but the territories were not mutually exclusive.

Although most feeding occurs on territories, many birds feed also on undefended neutral areas, favorite sites being dry playas (round, shallow basins) scattered throughout the breeding area.

### Aerial Displays

Territorial males frequently call from the ground and while performing an aerial display. The Wee-wee Call consists of a *wee-wee-wee* series. In the Falling Leaf Display, the bird flies to a height of about 5 to 10 m and suddenly holds its wings up over the back in a deep V (Figure 3), then floats back to the ground in this position. As the bird descends it rocks back and forth like a falling leaf. The Wee-wee Call begins just as the bird reaches the apex of the flight and continues until it reaches the ground.

A common aerial display among plovers is the Butterfly Flight in which the wing-beats are deep and slow compared to normal flight (Phillips, 1972). I saw the Mountain Plover perform this display on only four occasions and each time the display was brief. This plover apparently accomplishes its aerial advertisement primarily with the Falling Leaf Display rather than the Butterfly Flight.

Both sexes in the Mountain Plover give the Falling Leaf Display but I observed females performing it only after they were mated. Whether unpaired females perform this display is uncertain.

## *Agonistic Behavior*

Both sexes show similar agonistic behaviors, although males behave more aggressively. Territorial males first react aggressively toward all conspecific intruders, but if the intruder is a female, courtship usually develops.

### Horizontal Threat Display

The Horizontal Threat occurs when territorial holders confront intruders, serves to maintain individual distance, and is sometimes directed by a male toward his mate (see page 78). The most common agonistic display

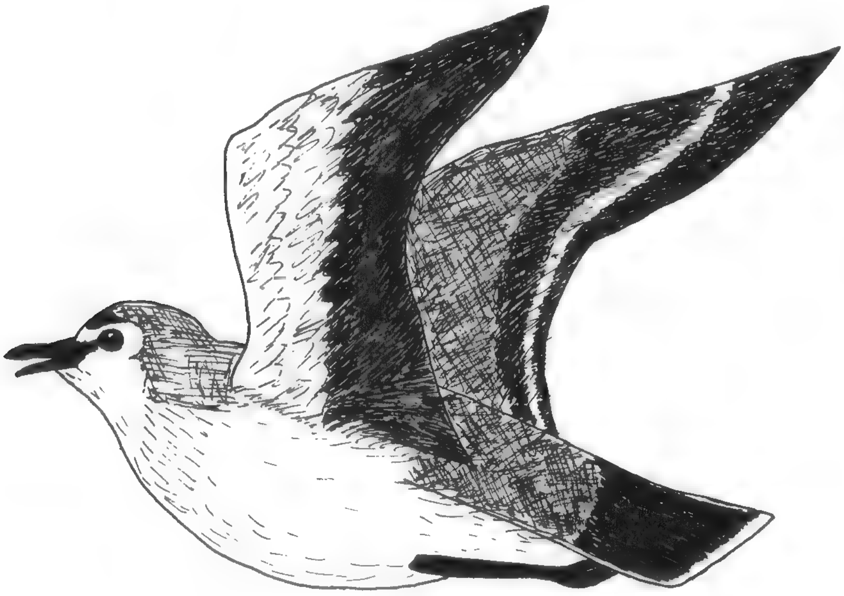

Figure 3. Falling Leaf Display. This posture is maintained as the performing bird floats back to the ground.

is the Horizontal Threat, which occurs in many plover species (Phillips, 1972). In this display the head, body, and tail are horizontal while the head is pulled in against the shoulders, the tail spread, and the back feathers sometimes ruffled. The feathers on the underside are compressed dorsoventrally and spread laterally to cover the wrists of the closed wings (see Graul, 1973 for illustration). The bird moves in a slow, gliding motion produced by low amplitude, high speed leg movements. Sometimes the Wee-wee Call accompanies the Horizontal Threat; at other times the display is given silently.

When a territorial male approaches an intruding male in this posture, the intruder usually moves away quickly. Sometimes the intruder moves away slowly, giving the Horizontal Threat, which results in a chase, either on the ground or in the air, as the trespasser is driven from the territory. In ground chases, the intruder invariably tilts the spread tail toward the pursuer, and sometimes the pursuer does the same. In aerial chases, the birds commonly fly away calling *Kip-Kip-Kip*. Aerial chases commonly cover a 65-hectare area and last up to 30 seconds. At the end of a chase, the pursuer usually returns to its territory and performs the Falling Leaf Display.

## Parallel Run Display

Whenever two territory owners come together at a territory border, Parallel Runs usually develop, as described for the Killdeer, *Charadrius vociferus* (Phillips, 1972). In such encounters, two birds run parallel about one meter apart. Commonly, one bird suddenly turns around 180 degrees and proceeds in the opposite direction with the other in pursuit. These encounters often last 10 to 15 minutes; I recorded one that continued for 40 minutes.

Some territorial males repeatedly engage in Parallel Runs with a particular neighbor, while ignoring intrusions by others. One marked male in 1972 interacted with another male at one segment of his territorial border four or five times daily. The marked male succeeded in expanding his territory about 40 m through these aggressive encounters. On three occasions, he ignored another male intruder, even though the intruder courted the marked male's mate.

A paired female may react to Parallel Runs between her mate and another male. On four occasions, when an aggressive male came within one meter of the female, she crouched.

Fights sometimes occur during Parallel Runs. The attacking bird jumps up and tries to grab the back of the opponent and may pull out some feathers. Sometimes both opponents leap-frog over each other in an attempt to grab the back of the other. Blows are also delivered with the wrist of the wing.

Throughout all kinds of aggressive encounters both combatants frequently give the Wee-wee Call.

Prolonged Parallel Runs with associated fights usually end in one of two ways. If the opponents are equally matched, the encounter ends when both birds move away from each other at about a 45-degree angle. If one wins an encounter, it will chase the loser by a flight pursuit as described earlier.

## Upright Threat Display

Frequently during Parallel Runs, both combatants suddenly stop and face each other in an Upright Threat Display (Figure 4). In this posture, the head is held high and the neck sleeked; the tail may or may not be spread, and the crown feathers sometimes are erected slightly. Both birds at times remain almost motionless in this posture for 10 to 15 seconds.

The relative frequency of these aggressive displays during the pre-

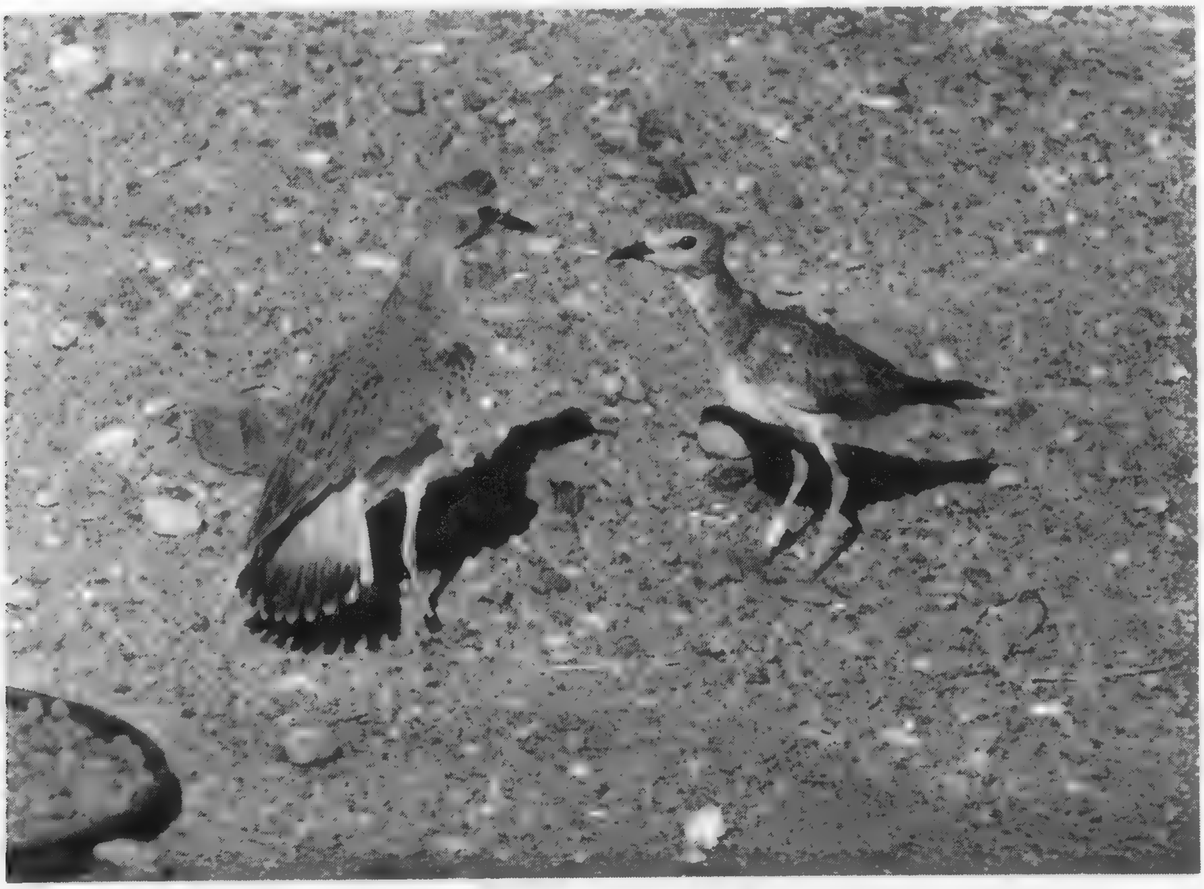

Figure 4. Upright Threat Display. The captive bird on the left is giving a high intensity form of this display. Although the crown feathers are sometimes erected, the erection is exaggerated in this photograph because of a previous injury to the crown region.

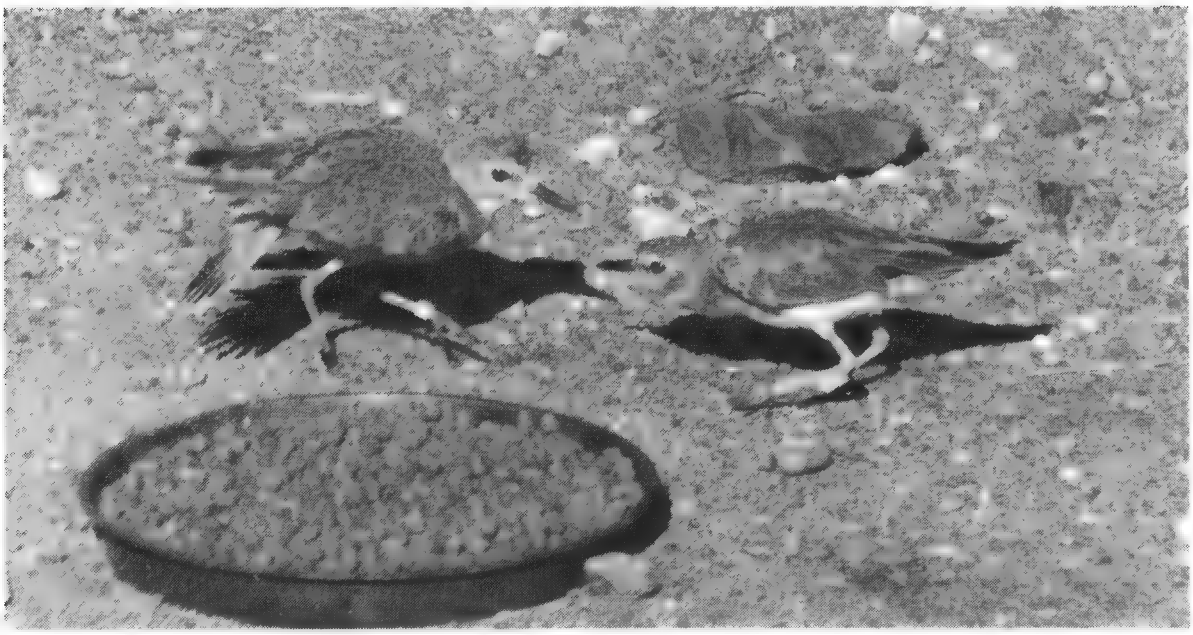

Figure 5. Two aggressive displays. The captive bird on the left is performing the Tail-down Rush and the bird on the right is performing the Head-down Threat.

nesting and early nesting periods was recorded between 30 March and 19 April 1969. The scores indicate "display bout frequency," but ignore time, so that a Parallel Run lasting 40 minutes counted the same as one lasting two minutes. This procedure yielded the following totals: Horizontal Threat, 186; Parallel Runs, 37; Upright Threat, 26; Fights, 27; Ground Chases, 25; Aerial Chases, 15.

### Other Agonistic Displays

Although the above aggressive displays are the only ones that I saw in territorial encounters in the wild, I observed two additional displays in captives during their first year. The most common aggressive display was the Head-down Threat (Figure 5). Captives also performed an intense aggressive display, the Tail-down Rush (Figure 5). This display is given occasionally in the wild by an adult threatening intruders at the nest, such as conspecifics, other small birds, and humans.

## *Courtship Behavior*

Throughout this paper, "courtship" refers to those events leading up to copulation. Essentially, males do the courting and females move from male to male before pairs are formed. In 17 out of 19 cases of courtship leading directly to copulation, the male initiated the courtship sequence.

Males normally begin courting only in the presence of a conspecific, although I once recorded a male courting in the apparent absence of another bird. Generally, a male will only court females, but occasionally a male begins courting a distant male until the mistake is realized.

### Scraping

Scraping is the most common courtship display and has been described in detail for other plovers (Phillips, 1972; Laven, 1940; Simmons, 1953). In this display the plover presses the breast on the ground, pushes back each

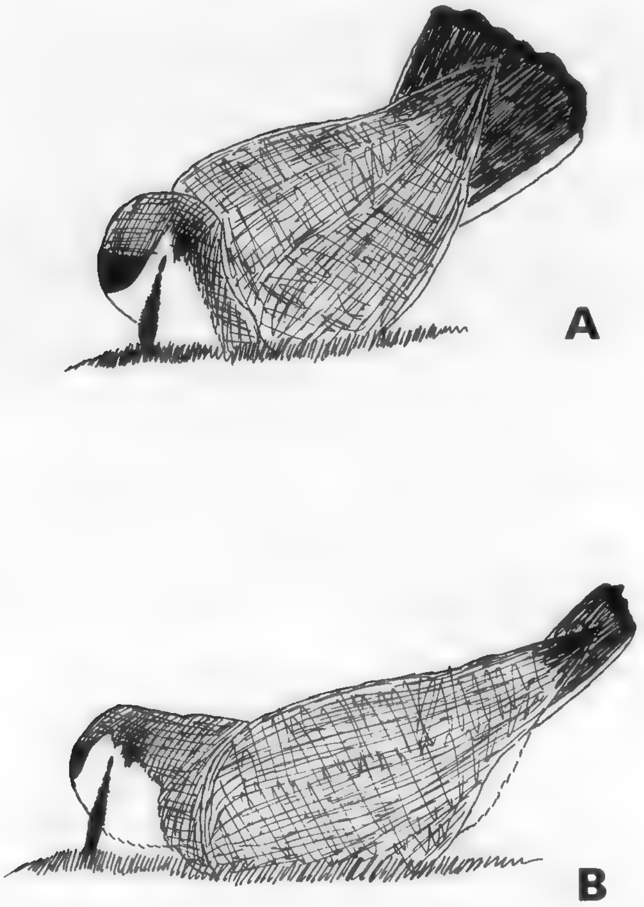

Figure 6. Bowing Display. Sitting form of the display, showing two views, oblique (A) and side (B). Illustration traced from a 35 mm slide.

foot alternately, and moves the spread tail up and down. The Mountain Plover uses two distinct signalling, or flagging, patterns: (1) it waves the tail successively in three rotating positions — left, center, right; or (2) waves the tail in the central position only. A scraping male does not appear to orientate the tail toward the female; instead he changes position in the scrape frequently, each change usually involving a rotation of about 90 degrees. Scraping produces nest bowls and there are many of these scattered throughout the territory. Some of these sites are used repeatedly by a male during courtship.

## Bowing

Bowing (Figure 6) is a courtship display performed in a standing or sitting position. It has not been described for any other species, although a similar display occurs in several shorebirds, according to R. E. Phillips (pers. commun.), including the Banded Dotterel (*C. bicinctus*), New Zealand Dotterel (*Pluvialis obscura*), and Wrybill (*Anarhynchus frontalis*). During Bowing, the tail is first spread and tilted towards the potential mate. As the tail reaches the spread position, the plover lowers the head, pointing the bill downward, expands the throat, closes the eyes, and gives a low Mooing Call. The head is then brought back to the starting position as the tail folds shut. The bird repeats these movements several times during a bout of Bowing. Each display lasts for about one second. Bowing is predominantly a male display, but I saw it performed once by a female in response to Bowing by a male.

### Sideways Displays

Nest-building movements are also used as elements of courtship and two types can be distinguished. In the Sideways Throwing Display, described by Lind (1961) in the Black-tailed Godwit (*Limosa limosa*), the standing bird throws nest material along one side of the body in repeated, quick movements. The Sideways Building Display, described by Moynihan (1953) for the Black-headed Gull (*Larus ridibundus*), involves the same movements as in Sideways Throwing, except that the bird is in a sitting position.

### Display Frequency and Female Responses

Using the method described earlier (see page 75) for counting the aggressive displays, I tabulated the relative frequency of these courtship displays, obtaining the following scores: Scraping, 227; Bowing, 48; Sideways Displays, 84. The high incidence of Scraping in these samples is understandable, since a male generally starts a courtship bout with Scraping, and in many early bouts the courtship proceeds no further. If a female responds to the initial Scraping of a male, the relative frequency of the displays can vary. For instance, on one occasion I tallied the displays given by a male in a single courtship bout with a female that had been with the male for at least three days. The talley was as follows: Scraping, 24; Bowing, 21; and "nest building," 16.

A male in the presence of a female may court repeatedly all day, only stopping briefly to rest or feed or drive away an intruder. Most courtship, however, does not result in copulation. Of 127 courtship sequences lasting at least three minutes each, 80 per cent ended without copulation, and the birds proceeded to feed or rest.

When a female responded positively to a courting male, one of three events followed in 25 courtship sequences observed that led to successful copulation: (1) the female initially replaced the male in his "scrape-site" (13 cases); (2) the female merely scraped near the male as he continued to scrape (9 cases); and (3) the male mounted without scraping by the female (three cases).

In a scrape exchange (Figure 7), the replacing bird approaches the scrape in the Head-low Display at a right angle to the side of the bird in the scrape. The head is lower than the back, the flank feathers are spread, and the open tail may or may not be tilted. The throat is enlarged. I have not heard a call, although it may well occur. A male being replaced invariably performs the Tilt Display, raising the outer wing, lowering the head, while slightly spreading the tail. The Tilt Display is similar to Bowing, with the wing-raising component added. Occasionally, a female replaces a male in a scrape and is then replaced, in turn, by the male. In these cases, the replaced female usually does not Tilt. I recorded one case of Tilting in a wild female; captive females Tilted occasionally. In general, Tilting, as with Bowing, is mainly performed by males.

The Kentish Plover, *Charadrius alexandrinus* (Rittinghaus, 1961; Boyd, 1972), and the Banded Dotterel (R. E. Phillips, pers. commun.) both have Tilt Displays.

### Mounting and Copulation

In the Mountain Plover, the scrape exchanges end when the female moves away, the male following her in the Head-low posture (see page 75).

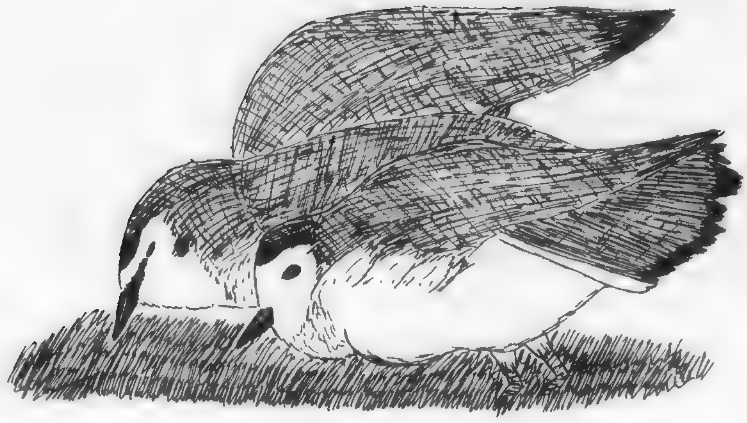

**Figure 7. Scrape Exchange. Female is giving the Head-low Display as she approaches the male, which is performing the Tilt Display with wing raised. Illustration traced from a 35 mm slide.**

When he nears her, he goes into the Upright Precopulatory posture (Figure 8) as he gives a low *chert-chert* call. If the female stops, the male makes rapid foot movements, "marking time," while in the Upright Precopulatory posture, and moves back and forth behind the female until she crouches.

After the male begins following her, if the female does not stop and crouch within about five to ten meters, the male turns away at a right angle to the female's direction of movement and moves off in a Horizontal Threat. At this point both birds usually feed or preen, although the male sometimes starts courting again within a few minutes.

If the female does stop and crouch, the male mounts promptly (Figure 9), and continues to shuffle his feet while resting on his tarsi on the female's back. The average mount-time prior to coition was five minutes and 21 seconds ($n = 31$), the shortest time being 46 seconds, and the longest just over 13 minutes. The male's tail does not pass around the side of the female's until just before he dismounts. Thus, although the mount-time is long, coition seems to be brief.

The Mountain Plover's average mount-time is the longest that has been recorded for any shorebird, although it sometimes reaches four minutes in the Wrybill (R. E. Phillips, pers. commun.), and three minutes in the Sanderling, *Calidris alba* (Parmelee, 1970).

Following coition, the male moves away quickly in the Horizontal Threat. Commonly, the female resumes feeding or preens, but on one occasion, a female attacked the male following copulation. Within a few minutes, the female commonly scraped for a few seconds after copulation. Precopulatory and postcopulatory behavior are summarized in Figure 10.

Copulations took place any time of day and I even observed one copulation at night, about one hour after darkness. I also heard birds giving the Wee-wee Call at night, so the study of night activity needs more attention.

## Pair-bond Formation

Although females initially visit the territories of several males, observations in 1969 and 1972 indicated that females soon develop preferences for certain males. In 1969, dawn to dusk observations on 13 unmarked male and female "pairs" showed that the birds remained together throughout the day on 11 of the days. One day a male and female copulated early in the morning, after which the female left and never returned. On another occasion, a male courted a female in the morning, and the female left and failed to return.

In 1972, I spent the prenesting period following five marked females and their respective mates. One of these females was with a marked male, one was with a male possessing a noticeable neck injury, two were accompanied by males with distinctive markings, and I could not identify the last female's mate.

The latter female usually stayed within 100 m of where I found her on a nest in 1971, but she frequently flew to two additional locations, each 300 m from her 1971 nest, but in different directions. In all these locations, a male courted her, but I have no way of knowing whether it was the same male each time. On four occasions, I watched her copulate within 100 m of her 1971 nest. I was unable to find her on a nest in 1972, so I do not know her eventual fate. I cannot rule out the possibility that she did not remain with one male.

Observations of the other four marked females confirmed that each female usually stayed with a single male. Each of these females spent most of the time with one male for at least 18 days prior to egg-laying. Commonly, however, during the first two weeks after a female settled on a territory with a male, one bird was absent for two to three hours. Often, one moved off to feed while the other slept, and on several occasions, the female flew off to feed in a neutral area while the male engaged in a prolonged territorial encounter with a neighboring male. As the laying period approached, however, the mates spent more and more time together.

The term "pair-bond" is usually applied where a male and female tolerate each other at close quarters and perform sexual behavior (Hinde, 1956), and in Black-tailed Godwits, Lind (1961) noted that members of pairs fly about together, feed together peacefully, copulate, and engage in scrape-reliefs. Most Mountain Plovers certainly form initial pair-bonds, since they meet the preceding criteria and both birds sometimes join in driving out territorial intruders. Furthermore, I never saw a marked bird copulate with a bird other than the mate during the prenesting period, although a "paired" male occasionally courted a strange female in the absence of his mate.

Initial pair-bonds, however, do not appear to be as strong as those formed in some other plovers. For instance, in the Killdeer (R. E. Phillips, pers. commun.; Graul, pers. observ.), aggression between members of a pair is rare and copulations occur frequently. In contrast, I observed a pair of

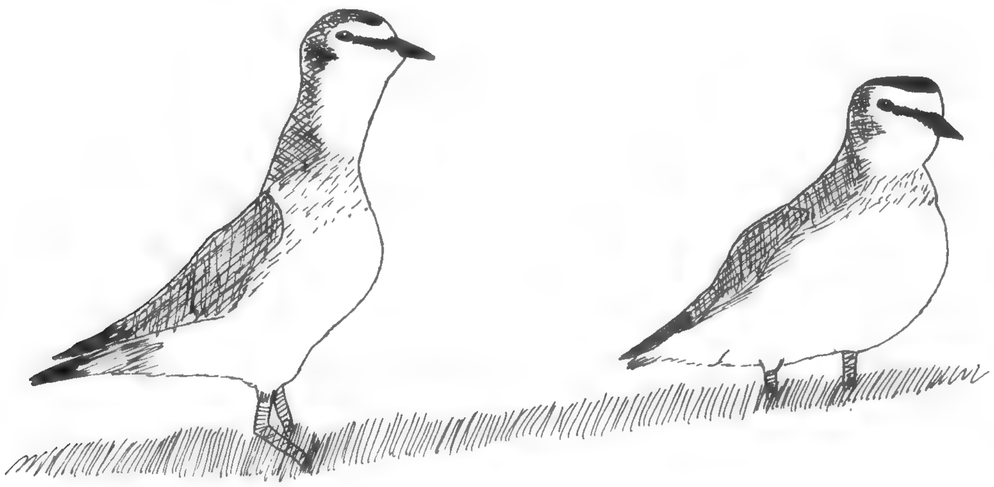

Figure 8. Male on the left is performing the Upright Precopulatory Display as he approaches the female. Traced from a 35 mm slide.

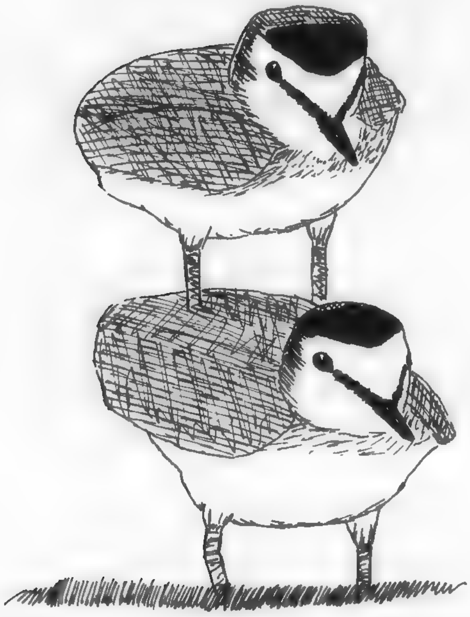

Figure 9. Male mounted on a female prior to coition. Traced from a 35 mm slide.

Mountain Plovers copulating twice in the same day on only two occasions (based on 21 dawn-to-dusk watches). Paired males continue to perform the Horizontal Threat whenever females fail to stop and crouch after a scrape exchange. Furthermore, on one occasion, a female attacked her mate following copulation. In fact, pair-members generally maintain their 6 to 15 m individual distance as they move about as a unit.

The relatively long mount-time may be an indication of a high level of aggression between male and female, the long period being necessary to overcome the aggression between the members of a pair. Alternatively, the long mount-time may just serve to reinforce the weak pair-bond. A comparison with other species is needed to evaluate these speculations.

## *Nesting Behavior and Multiple Clutches*

Although pair-bonds initially are formed and territories are defended, social relationships become complex once egg-laying commences. To illustrate these complexities, I will first describe two case histories based on the 1972 marked females:

### Case History One

*1 April–16 April.* Female A remains with Male A (neck injury) on a territory of about 16 hectares and they copulate almost daily.

*17 April.* Male A sits on nest (one egg) at 13:50 hours.

*18 April.* Male A sits on nest (two eggs) at 12:10. At 13:00 he joins Female A, copulates, and then returns to the nest.

*19 April.* At 06:30 hours Female A lays a third and final egg (a normal clutch-size). Male A sits on nest at 12:30. At 15:15 he joins Female A and I sprinkle green "Thief Detection Powder" in the nest cup.

*20 April.* At 06:30 Male A (now green) is courting Female A.

*21 April–22 April.* Male A continues to tend nest and to associate with Female A.

*23 April.* Female A being courted by a strange male on an adjacent territory, but no copulation is observed.

*24 April.* Male A copulates with unmarked female about 200 m south of his initial territory.

*25–29 April.* Male A continues to associate and copulate with Female A, while also incubating at Female's A's first nest.

*30 April.* At 10:00 hours Female A briefly visits second nest (one egg) that is 120 m from the first nest (both nests in initial territory).

*1 May.* At 10:30 Female A sits on second nest (two eggs).

*2 May.* Female A on second nest at 10:30 and 14:00.

*3 May.* Female A on second nest at 10:30 and 14:00.

*4 May.* I remove the two eggs from the second nest at 13:50.

*5 May.* Female A is being courted by Male B at 13:15 on adjacent territory. Male B had been marked at a nest on this adjacent territory on 29 April and was initially paired with another marked female.

*9 May–15 May.* Female A continues to associate and copulate with Male B in an area where their initial territories overlap. Male A is almost exclusively occupied with incubation at Female A's first nest.

*15 May.* At 11:00 hours Female A is incubating at the nest (three eggs) in her initial territory. This nest is 150 m from her second nest, in the direction of Male B's territory, and only 30 m from where she was banded on a nest in 1971. Female A found incubating at 13:10, 18:00, and 23:00.

### Case History Two

*2 April–27 April.* Female C remains with Male C (banded) on sixteen-hectare territory where they copulate almost daily.

*28 April.* Male C briefly visits nest (one egg).

*29 April.* Nest has two eggs at 13:00 hours.

*30 April.* Female C lays third egg at 08:30.

*1 May.* Male C on nest at 09:00, but Female C is 300 m away, near the edge of the initial territory, being courted by Male D (unmarked).

*2 May.* Female C remains with presumed Male D in area where their initial territories overlap. Male C continues incubation.

*3 May.* At 11:20 presumed Male D goes through scrape exchange with Female D (unmarked) about 150 m from where Male D and Female C have been staying. Within a few minutes, Female D leaves and Male D returns to Female C. The scrape-exchange location is a nest (Nest Two) with one egg.

*5 May.* Nest Two contains two eggs at 10:45.

*6 May–7 May.* I maintain continuous dawn-to-dark observations at Nest Two and also keep track of Male D and Female C. On four occasions, Male D walks toward Nest Two with Female C following. Each time the pair approaches to within 30 to 50 m of the nest, Male D suddenly attacks Female C and forces her to fly back to the opposite end of his territory (the area where their initial territories overlap). Upon alighting each time, Male D immediately starts courting Female C, and on two occasions they copulate. On six occasions, Male D incubates at Nest Two while Female C rests in another part of the territory.

*7 May.* The unmarked female visits Nest Two and lays the third egg at 19:14. An unmarked male tries to court her while she is on the nest, but she repeatedly attacks him and he leaves. This male is not Male D, since the latter is with Female C about 200 m from Nest Two. After laying, the unmarked female flies about 200 m south.

*8 May.* At 08:30 I place green "Thief Detection Powder" in Nest Two. At 09:00 Male D visits nest briefly and is marked "green." He then returns to court Female C.

*9 May–10 May.* Male D continues to associate with Female C and periodically incubates at Nest Two alone (based on four day-checks and two night-chceks).

*11 May.* Female C being courted by Male E (unmarked) 400 m north of her initial territory at 12:00.

*12 May.* Female C again being courted by unmarked male (at 10:30) in same area as on 11 May. I watch this male all day and he never goes to a nest.

*14 May.* Female C is alone at 09:30 in area where her initial territory overlaps Male D's territory.

*15 May.* Female C goes to a three-egg nest (Nest Three) at 18:45 in the area of territory overlap.

If we can assume that the female laid all the eggs in the clutch at a rate of one egg per day, I calculated that the female in Case History One started laying her second clutch not more than 11 days after the completion of her first, and initiated her third clutch not more than nine days after I removed her second clutch. The female in Case History Two started laying her second clutch not more than 13 days after the completion of her first.

In these case histories, four females laid clutches incubated by the males alone, and at least two females then laid a second clutch that they incubated themselves. One of these females switched mates prior to laying her second clutch; the other remained with her original mate while she laid her second clutch, but did switch mates prior to laying a third replacement clutch. Furthermore, at least three males copulated with more than one female. Both females that laid more than one clutch placed all clutches within their initial territories, although males were available on other territories.

There is additional evidence that males copulate with more than one female. In one instance, I watched a male, attending a two-egg clutch, copulate with a female. I then immediately collected the female. She had one egg in the oviduct and two large ova in the ovary. The next day, a third egg had been added to the male's nest — obviously laid by a different female. I have also recorded an additional case of an incubating male attacking a female near the nest, but courting her away from it. This supports the observation in Case History Two (see page 81).

Several observations indicate that the findings in the two case histories are not exceptional. In 1969, in the three weeks prior to egg-laying, I made nine counts of Mountain Plovers on an area of 64.77 hectares (812.3 × 812.3 meters). I covered the area in a car by making transects at 100-meter intervals. Mountain Plovers can often be seen at 200 meters. I initiated all counts at 06:30, since the birds are especially active at that time. Counts of 22 to

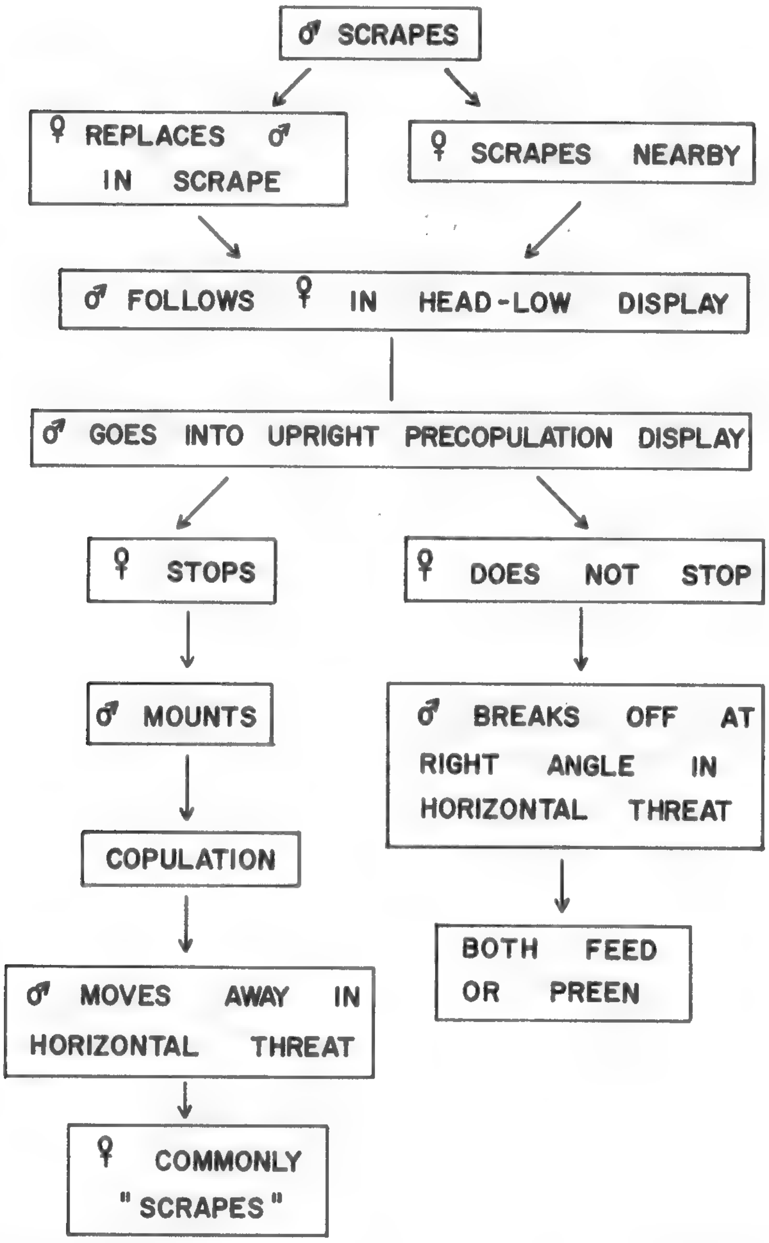
♂ SCRAPES
♀ REPLACES ♂ IN SCRAPE
♀ SCRAPES NEARBY
♂ FOLLOWS ♀ IN HEAD-LOW DISPLAY
♂ GOES INTO UPRIGHT PRECOPULATION DISPLAY
♀ STOPS
♀ DOES NOT STOP
♂ MOUNTS
♂ BREAKS OFF AT RIGHT ANGLE IN HORIZONTAL THREAT
COPULATION
BOTH FEED OR PREEN
♂ MOVES AWAY IN HORIZONTAL THREAT
♀ COMMONLY "SCRAPES"

Figure 10. Summary of the most common sequences of behavior associated with copulation in the Mountain Plover.

31 birds were made on each census, with an average of 26. I later found 27 nests on this area, 21 of them active at the same time. I cannot be certain that these counts of birds and nests were complete, but there is close agreement with the findings in the two case histories.

Additional observations indicate that only one adult normally tends each nest and brood, and that the attending bird may be either sex. I made 80 day-checks and 13 night-checks on 43 marked adults attending either nests or broods, and never found any evidence of more than one adult per nest or brood. Furthermore, "Thief Detection Powder" placed in six nests with completed clutches always resulted in only one marked adult per nest (no two markings are exactly alike). The sex of birds attending nests or broods was confirmed by collecting the bird or by observing copulations in 38 cases, revealing 16 females and 22 males.

Bailey and Niedrach (1965) felt that the two adults shared incubation at a nest, but they did not study marked birds. In view of my results, I find their evidence unconvincing, especially since individual birds react quite differently at the nest at different times of day.

Although all of the preceding observations complement the findings in the two case histories, I did record two observations which may represent exceptions. In 1969, the earliest nest found contained one egg on 17 April. On 20 April, a female copulated and then went to another nest containing one egg. A male approached the female on the nest three times and each time the female attacked him. Finally, after the female left to feed, the male settled on the eggs briefly and then followed the female. I confirmed the sex of this incubating adult — a female — by collecting it at the nest 11 days later. Thus, it is possible that the female took over her own first clutch.

In another instance a female attended her nest during egg-laying, but a male assumed incubation at this nest alone once the clutch had been completed. I do not know if these two birds were initially paired.

Although further research is needed to document the extent of variability in the Mountain Plover social system, such variability may be expected, based on what we know about other shorebird social systems. For instance, both the Lapwing (*Vanellus vanellus*) and European Golden Plover (*Pluvialis apricaria*) are considered monogamous, but Rinkel (1940) and Wilson (1967) report that some Lapwing males are bigamous or trigamous, and Bannerman (1961) reports cases of bigamy in the European Golden Plover. Jenni and Collier (1972) found that in the American Jacana (*Jacana spinosa*) some females lay clutches for more than one male in a season, but other females do not. Finally, Pulliainen (1970) reports that while only the male Dotterel (*Eudromias morinellus*) usually tends the eggs and young, sometimes these duties are shared by both pair-members.

## *Similar Breeding Systems in Other Birds*

Jenni (1973) reviewed avian social systems in which females commonly lay more than one clutch in rapid succession. In these systems, females either lay clutches that are incubated by more than one male (polyandry), or they lay one clutch attended by a male and a second which they attend themselves. Since there is no term for both of these strategies, I will refer to them as "rapid multi-clutch systems."

Research on rapid multi-clutch species has resulted in several hypotheses that may explain the evolution of the Mountain Plover social system. Jenni and Collier (1972) proposed that polyandry in the American Jacana might be an adaptation to a low food supply, since this mating system reduces competition for food by allowing fewer adults to maintain the same reproductive output as more adults.

Selander (1972) also proposed that polyandry may have evolved as a response to low food conditions, placing a premium on one member of the pair leaving the territory to reduce food competition; which member leaves is largely a matter of chance. Nethersole-Thompson (1973) proposed that, in the Dotterel, the female leaves the parental duties to the male because, under low food conditions, the female lacks the energy to participate in parental duties after the heavy expense of egg production. This reasoning is supported by studies on other bird species, which show that egg production is affected by food shortages, whereas sperm production remains constant, short of starvation conditions. This implies that egg production requires much more energy than sperm production (King, 1973).

Jenni (1973) noted that the nature of the food supply and high predation rates may be involved in the evolution of polyandry, and Oring and Knudson (1972) stressed the same factors in discussing the evolution of the polyandrous system in the Spotted Sandpiper (*Actitis macularia*).

Interestingly, most of the preceding suggestions stress low food supply as the factor promoting the initial reduction in female participation in parental duties, which is a necessary prerequisite for the evolution of a rapid multi-clutch system (Jenni, 1973). Standing alone, however, a low food hypothesis does not fully explain the evolution of a rapid multi-clutch system. It emphasizes the inability of females to lay and aid in the parental duties, but all rapid multi-clutch systems are based on females having enough resources to produce more than one clutch. When food is abundant enough for a female to lay more than one clutch, selection on a female to leave the parental duties of incubation to her mate might be just as strong as selection favoring the same strategy at low food levels, since this strategy would allow a female to lay additional clutches.

In the Sanderling, the female lays a clutch presumably incubated by a male and a second clutch which she incubates herself. Parmelee and Payne (1973) postulated that this breeding system may be adapted to the extreme fluctuations in food levels that occur in the high arctic. They suggested that this system allows females to adjust their reproductive efforts to food conditions. This hypothesis stresses selective pressures that both reduce parental duties of females under low food conditions and increase the probability of additional clutches whenever possible. It is also advantageous to males, since if females were free to lay multiple clutches, a male's chances of fertilizing more than one clutch increase.

I suggest that this low food-high food hypothesis may explain the evolution of the Mountain Plover social system. In the next sections I will argue that extreme food fluctuations occur on the shortgrass prairie, and I will discuss the impact of these food fluctuations on the evolution of the Mountain Plover.

## *Food Fluctuations in the Shortgrass Prairie*

Mountain Plovers eat insects (Baldwin, 1971). Although conclusive evidence is lacking, it is likely that extreme fluctuations in insect food occur on the shortgrass prairie in response to fluctuations in precipitation on a yearly, seasonal, and area-to-area basis.

The annual fluctuations in precipitation are known to be more extreme on the shortgrass prairie than in other grassland areas. In shortgrass areas, one out of every 12 years may differ from the long-term precipitation average by at least one-half the average; in tallgrass areas, such extremely wet or dry years average only once in every 42 years (Wiens, pers. commun.).

The shortgrass prairie climate is also the most unpredictable of grassland climates in terms of seasonal precipitation patterns (Wiens, pers. commun.). The variations in precipitation in April and May are of particular interest, since this is when most egg-laying occurs. I have analyzed the precipitation records for the last 31 years for these two months at New Raymer, Colorado, 19 km east of my study area. The April average is 3.35 cm, ranging from 0.5 to 11.7 cm; the May average is 6.12 cm, ranging from

0.8 to 14.7 cm. April precipitation in 11 of the 31 years, and May precipitation in 13 of these years differed from the long-term monthly averages by at least one-half the average.

Mitchell (1971) discussed the precipitation variability on an area-to-area basis on the shortgrass prairie and noted that large variations occur between pastures located short distances apart, although he gives no details. He attributed these variations to the restricted nature of the storms.

Wiens (pers. commun.) notes that precipitation on the grasslands is frequently correlated with primary production, and thus food supplies for birds in general. In fact, as precipitation increases across the grasslands, so does avian standing crop biomass (Wiens, 1971).

Tomanek and Hulett (1970) presented additional suggestive evidence that food (insects) at times may be low on the shortgrass prairie. They reported that on heavily grazed areas near Hays, Kansas, there was a 90 per cent reduction in the original basal cover during the 1952 to 1956 drought. They also reported that in a 27-year period on this same area, primary production ranged from 101 kg of grass per hectare to more than 460 kg, production being correlated with precipitation. Although evidence is lacking that insect abundance correlates with precipitation and primary production on the shortgrass prairie, I suspect that this is the case.

Droughts are common on shortgrass prairies, presumably causing a scarcity of food for Mountain Plovers. Weakly (1943) analyzed tree-ring growth over the last 400 years on the shortgrass prairie in western Nebraska and found that droughts last an average of 13 years each and are separated by an average of 12.5 years.

A drought began in June 1971 on my study area. A comparison with the same month two years earlier when no drought existed shows some marked differences in breeding. In June 1969, the mean maximum temperature was 24° C and precipitation totaled 80.5 mm. In June 1971, the mean maximum temperature was 29.5° C and precipitation totaled 53.3 mm. Of 15 nests active on 14 June 1969, none was abandoned, but of 11 nests active on the same date in 1971, five were subsequently abandoned. Although insect data are not available for 1969, in 1971 there was over a 70 per cent decrease in soil macroarthropod biomass from 5 May to 15 June (Lloyd, pers. commun.).

Reduced clutch sizes and unusually long intervals between the laying of eggs might also be expected to result from reduced food levels. Both phenomena occur in the Mountain Plover, but my data are too few to show such correlations. The clutch size is normally three (105 of 133 nests), but 17 nests contained only two eggs.

Mountain Plovers usually lay eggs at one- to two-day intervals, but I recorded two cases during drought periods (1971 and 1972) in which at least four days elapsed between the laying of the second and third (last) eggs. Such delays might be expected during inclement weather, but these two instances both occurred during favorable weather periods.

During periods of good rainfall, insect abundance may at times be high in grasslands. Verner and Willson (1966) noted that all solar radiation entering grassland systems is absorbed in a narrow stratum and suggested that this results in high food availability on a per unit area basis. In view of the extreme fluctuations in precipitation and primary production, it seems likely that food is sometimes abundant on the shortgrass prairie. If it is

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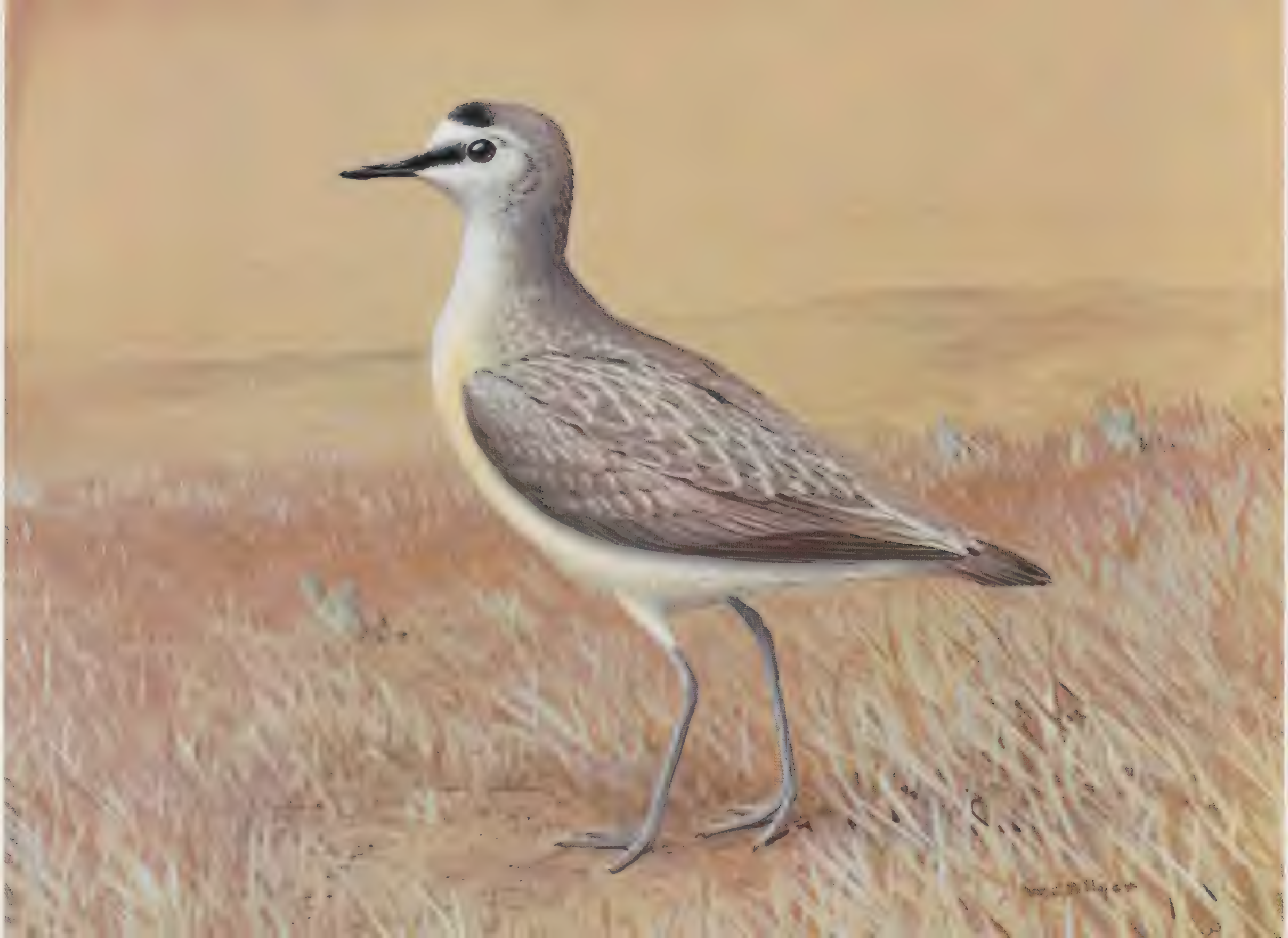
**Mountain Plover, *Charadrius montanus*. Painting by William C. Dilger.**



correct, however, that food on the shortgrass prairie is also sometimes extremely scarce, then I would modify Verner and Willson's proposal as follows: food levels are potentially high on the shortgrass prairie, but whether or not this potential is reached depends upon the amount of rainfall.

## *Food Fluctuations and Evolution of the Plover Breeding System*

### Egg Production

Within the subfamily Charadriinae, some species lay four eggs, some three, and others two (Maclean, 1972). In the model of evolutionary relationships proposed for this group by Bock (1958), all of the close relatives of the Mountain Plover lay three eggs. If Bock's model is correct, then it is likely that the ancestral stock giving rise to the Mountain Plover had a clutch size of three eggs.

The Mountain Plover lays relatively small eggs with a relatively low biomass per clutch (Table 1). Small egg size characterizes most species of shorebirds in which females lay multiple clutches. Jenni (1973) interprets this as an adaptation to enhance the ability of females to lay additional clutches. Parmelee and Payne (1973), however, proposed that the small eggs laid by the Sanderling might allow a female to lay a clutch under conditions of poor food supply without greatly increasing her chances of mortality. Laying three small eggs might also allow Mountain Plover females to reproduce under poor food conditions.

In fact, on the heavily grazed areas of my study area, relatively small clutches are laid by all of the top three avian species: Horned Lark (*Eremophila alpestris*), McCown's Longspur (*Rhynchophanes mccownii*), and Mountain Plover (Wiens, 1971). The Horned Lark lays an average clutch of 2.8 on my study area, although it commonly lays four eggs over much of its remaining range (Ronald Ryder, pers. commun.). The McCown's Longspur has an average clutch size of 3.2 on this area (Phillip Creighton, pers. commun.); this is the lowest clutch size within the Longspur group (Hussell, 1972). Thus, the reduced egg production of all three species might be adaptations to low food conditions.

### The Rapid Multi-clutch System

The optimal breeding strategies of the two sexes are rarely identical and a breeding system is usually a compromise between the differing optimal strategies of the two sexes (Trivers, 1972). Since Mountain Plovers do not feed their young and have a small clutch size, one adult commonly can perform all parental duties. If one adult is able to raise the brood alone, it might appear that either sex could leave the parental duties to the other. I will argue that under conditions of extreme fluctuations in food levels the female would be selected to forego parental care.

With extremely low food levels, assuming the high energy demands of egg production, there are at least two possible situations in which parental care by the male could be favored. In the first, females, on the average, cannot perform all parental duties, although males can raise some young alone. Under these conditions, selection would likely favor males remaining with their nests as long as possible and also females leaving the parental duties to their mates. In the second situation, either males or females can perform all parental duties alone, but males are selected to do so to enable females

## TABLE 1

### Relationship of Egg Weight to Adult Body Weight in Some Species of Charadriinae

| *Species*[1] | *Clutch size*[2] | *Egg weight (grams)*[3] | *Adult body weight (grams)*[4] | *Adult body weight (grams)*[5] | *Relative egg production*[6] |
|---|---|---|---|---|---|
| Ringed Plover<br>(*Charadrius hiaticula*) | 4 | 11.5 | 60.0 | 19.2 | 77 |
| Semipalmated Plover<br>(*C. semipalmatus*) | 4 | 9.6 | 45.0 | 21.3 | 85 |
| Golden Plover<br>(*Pluvialis apricaria*) | 4 | 33.0 | 200.0 | 16.2 | 65 |
| American Golden Plover<br>(*P. dominica*) | 4 | 26.0 | 130.0 | 20.0 | 80 |
| Black-bellied Plover<br>(*P. squatarola*) | 4 | 34.2 | 200.0 | 17.1 | 68 |
| Little Ringed Plover<br>(*Charadrius dubius*) | 4 | 7.5 | 40.0 | 18.7 | 75 |
| Piping Plover<br>(*C. melodus*) | 4 | 9.4 | 52.7* | 17.8 | 71 |
| Killdeer<br>(*C. vociferus*) | 4 | 14.5 | 91.3* | 15.8 | 63 |
| Wilson's Plover<br>(*C. wilsonia*) | 3 | 12.4 | 56.9* | 21.7 | 65 |
| Kentish Plover<br>(*C. alexandrinus*) | 3 | 8.9 | 43.0 | 20.6 | 62 |
| Caspian Plover<br>(*C. asiaticus*) | 3 | 13.8 | 62.3* | 21.2 | 63 |
| Large-billed Sand Plover<br>(*C. leschenaultii*) | 3 | 15.6 | 74.1* | 21.0 | 63 |
| Short-nosed Sand Plover<br>(*C. mongolus*) | 3 | 12.6 | 60.8* | 21.0 | 63 |
| Mountain Plover<br>(*C. montanus*) | 3 | 15.6 | 106.8* | 14.6 | 44 |
| Dotterel<br>(*Eudromias morinellus*) | 3 | 17.0 | 120.0 | 14.1 | 42 |
| Two-banded Plover<br>(*Charadrius falklandicus*) | 3 | 13.5 | 65.0* | 21.0 | 63 |
| Three-banded Sand Plover<br>(*C. tricollaris*) | 2 | 7.5 | 35.0 | 21.4 | 43 |
| Rufous-chested Dotterel<br>(*C. modestus*) | 2 | 22.0 | 79.7* | 27.6 | 55 |
| Collared Plover<br>(*C. collaris*) | 2 | 6.8 | 30.6* | 22.2 | 44 |
| Magellanic Plover<br>(*Pluvianellus socialis*) | 2 | 11.3 | 87.0* | 13.0 | 26 |

1. Classification follows Jehl (1968).
2. Data from Maclean (1972). See Graul (1973) for other literature sources.
3. Values are from Schönwetter (1967), except for the Mountain Plover, which are from the present study.
4. Values are averages of both male and female weights. Values followed by an asterisk are averages of data obtained from 2 to 15 specimens in the Bell Museum, University of Minnesota, or from the U. S. National Museum, Washington, D. C. Other values are from Schönwetter (1967). The sample sizes for body weight are small, but because of the large range of values among the species, the relative species relationships are probably fairly accurate.
5. This figure was obtained by dividing the weight of a single egg by the adult weight and multiplying by 100.
6. This figure was obtained as follows: (clutch-size × egg weight) divided by adult weight × 100.

to gather the energy reserves necessary for laying replacement clutches. Such a strategy might be favored in an area where egg-loss rates are high. In both of these situations, males are committed to increased parental care. Especially is this likely in regions where food conditions are subject to large changes, and where food reserves are more important for egg production than in areas of more stable climate and sources of food.

With ample food supplies, females, by not participating in parental duties with first clutches, are free to lay additional ones. In fact, because of the relatively invariable clutch size, laying more than one clutch is the only way they can increase their reproductive output in response to an abundance of food. Having females lay more than one clutch is also advantageous to males, since a male's probability of fertilizing more than one clutch increases if females are multiple-brooded (Parmelee and Payne, 1973).

Selection under conditions of erratic food supply, therefore, favors the female that relinquishes parental duties at the first nest. In contrast, a male, by failure to incubate the first clutch laid by his mate, might not increase his reproductive strategy. A female is more likely to be under selective pressure to leave the parental care of her first clutch to her mate if the benefit to the female outweighs any disadvantages to the male. The present explanation, therefore, differs from Parmelee and Payne's (1973) hypothesis only in that I assume that a rapid multi-clutch system could evolve even if it is somewhat disadvantageous to males. Jenni (1973) makes the same suggestion for the American Jacana.

### Females Incubating Second Clutches

The tendency for the female to assume the incubation of her eggs may be related to major qualitative differences between territories. It might be advantageous for a female to nest on a good territory (more food, better protective cover). Since males on good territories often are already attending nests, females frequently must incubate their own clutches laid on these territories. If so, some females conceivably could be assuming the parental duties at their own first nests. More data are needed to verify this hypothesis.

### Switching Mates

Sometimes it can be advantageous for females to switch mates, since the original mate might no longer be available when an additional clutch is ready to be fertilized. The original male's availability to the female will depend upon his energy requirements for attending the first clutch, his hormonal-gonadal condition, and the timing of the additional clutch. Such factors could explain why one female remained with her initial mate until she laid her second clutch, but switched mates prior to laying her third (see page 82).

### Aggression Between Members of a Pair

The high level of aggression sometimes shown between members of a mated pair may be related to their separate, simultaneous incubation of two clutches. Selection might favor a male on a nest trying to maintain a pair-bond with a female not associated with that nest. This female, however, probably does not contribute to the success of the male's nest; in fact, her presence might increase the chances of his nest being located by a predator, especially if she tries to place her eggs nearby. Similarly, a nesting female might be exposed to predation by having a male court her near her nest. Thus, a high level of aggression keeps other birds away from an active nest, but courtship elsewhere in the territory allows a male to maintain a pair-bond with a female not associated with his nest.

### Support for the Fluctuating Food Hypothesis

I have argued that the rapid multi-clutch system of the Mountain Plover evolved because this species does not feed it young, does not have a flexible clutch size, and inhabits an area characterized by extreme fluctuations in food supply. To support such a hypothesis, a comparison must be made with other species and their environments (Tinbergen, 1972).

Rapid multi-clutch systems are not common in birds and have been postulated or proven to occur regularly only in Rheidae (two species), Tinamidae (five species), Mesoenatidae (one species), Turnicidae (two species), Rallidae (one species), Jacanidae (two species), Rostratulidae (one species), Charadriidae (two species), Scolopacidae (three species), and Phalaropodidae (one species). See Jenni (1973) for references.

None of the above species feed their young, and almost half of them are shorebirds with relatively invariable clutch sizes. The clutch-size factor might explain why such systems are relatively uncommon. Most species with highly flexible clutch sizes can adapt to extreme fluctuations in food by varying the number of eggs laid.

Although there is reason to believe that extreme food fluctuations occur in areas inhabited by Mountain Plovers and Sanderlings (Wiens, 1971; Parmelee and Payne, 1973; Tomanek and Hulett, 1970), solid data are lacking on food habits for rapid multi-clutch species. Climatic variations are apparently great on the breeding grounds of the Dotterel (Nethersole-Thompson, 1973), and the American Jacana breeds on tropical ponds where food variations on a spatial and temporal basis may be great (Jenni and Collier, 1973).

In the Greater Rhea (*Rhea americana*), several females lay for a male, who then attends the eggs, and the females then lay for additional males (Bruning, 1973). Bruning notes that a female probably only lays four to six eggs per male because laying additional eggs would cause the chicks to hatch too far apart. Furthermore, he found that males frequently abandon their nests throughout the season and abandonment is almost universal once summer begins. This suggests to me that food at times may be extremely low relative to the energy demands required for incubation.

I conclude that fluctuations in food on the breeding grounds may provide the key to an understanding of avian breeding systems involving rapid laying of several clutches. The comparative advantages of the different types of rapid multi-clutch systems are not yet apparent, however.

## *Summary*

From 1969 to 1972, I conducted field studies during the breeding season on the social system of the Mountain Plover (*Charadrius montanus*) on the shortgrass prairie in northeastern Colorado.

Using marked birds, I found that in some cases, after forming an initial pair-bond, a female lays one set of eggs which the male tends alone and then lays a second clutch which she incubates. Some females remain with

their original mates, but others switch mates prior to laying the second clutch. Some males also copulate with more than one female.

I discuss various hypotheses which attempt to explain the adaptive significance of such breeding systems, and suggest that the Mountain Plover mating system evolved in response to extreme fluctuations in food on a yearly, seasonal, or area-to-area basis.

The reduced clutch size and small eggs of the Mountain Plover probably represent adaptations to low food. I suggest that under fluctuating food conditions female Mountain Plovers can greatly optimize their reproductive strategies by not participating in parental duties at their first nests, but that this does not apply to males. Based on the assumption that natural selection operates on the individual, I suggest that a female will take the above action as long as the advantage to her is not outweighed by any disadvantage to her mate. I also discuss the adaptive nature of other aspects of the Mountain Plover social system.

Finally, I propose that rapid multi-clutch systems may occur whenever a species does not feed its young, does not have a flexible clutch size, and inhabits an area characterized by extreme fluctuations in food supply. A comparison of rapid multi-clutch species and their habitats tentatively supports this hypothesis, but more data are needed for verification.

### *Acknowledgments*

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# PASSERINE BIRDS OF THE FALKLAND ISLANDS: THEIR BEHAVIOR AND ECOLOGY

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Black and white and color photographs by the author

In the Falkland Islands, a South Atlantic archipelago some 300 miles northeast of Tierra del Fuego at the southern extremity of South America, nine passerine birds are native and breed regularly. These are, in accordance with the terminology of Meyer de Schauensee (1970), the Blackish Cinclodes (*Cinclodes antarcticus*) that I have called Tussockbird in this article; Dark-faced Ground-tyrant (*Muscisaxicola macloviana*); Grass Wren (*Cistothorus platensis*), called in North America the Short-billed Marsh Wren; House Wren (*Troglodytes aedon*); Austral Thrush (*Turdus falcklandii*); Correndera Pipit (*Anthus correndera*); Long-tailed Meadowlark (*Sturnella loyca*), sometimes called the Greater Red-breasted Meadowlark; Black-throated Finch (*Melanodera melanodera*); and Black-chinned Siskin (*Spinus barbatus*). All of these species breed in southern South America as well as the Falklands.

While Mrs. Pettingill and I were in the Falklands during two austral springs and their succeeding summers, we watched all nine passerines on many occasions. Always we paid attention to their behavioral specialties and habitats chosen. Of special interest to us was how these essentially continental species coped with the limitations and peculiarities of the Falkland environment.

The body of this article is an account of our observations of the nine species, preceded by a description of the pertinent aspects of their environment and followed by a discussion with conclusions about significant matters concerning the species generally. My description of climate and weather is repeated in part from my earlier paper (Pettingill, 1960) on the effects of climate and weather on Falkland birds.

## *Environment of the Falklands*

### Geographical Features

The Falkland archipelago (Figure 1), between 52° and 53° S Lat., consists of two main islands, East Falkland and West Falkland, narrowly separated by a sound, and well over 200 small islands and islets, comprising altogether 4,618 square miles, or 2,903,100 acres of land surface. Both of the main islands have numerous hills, many reaching elevations between 1,000 and 2,000 feet and two as high as 2,264 and 2,297 feet. Nearly all feature rocky outcrops and a few have the so-called "stone runs" (Figure 2) of a few feet to hundreds of yards in width, made up of loose silvery gray boulders and sharp rocks that from a distance suggest streams pouring down the slopes. There are also flatlands, in some cases quite extensive. All of southern East Falkland is a low-lying plain without notable relief.

The soil is primarily peat. Water from the interior of East and West Falkland flows to the sea in shallow streams which, during their course, often meander sluggishly while flanked by steep peat banks several feet in height. Dotting the landscape are many ponds and lakes, usually the backwaters of stream systems, although some pools in the peat beds are year-round and without apparent inlets.

The coast of the Falklands has sharp contrasts in formation. There are numerous places where the turfed upland declines gradually seaward, terminating just above the high-tide line in low banks. Elsewhere are numerous places where the terrain drops to the sea in sheer cliffs, frequently from impressive heights (Figure 3). But it is more characteristic of the land to become increasingly broken as it nears the sea, descending finally by broad terraces upon which are massive accumulations of loose rocks and boulders. In its configuration, the coast is complicated not only by the vast array of islands but also by the vast number of inlets, harbors, and sounds extending far into the interiors of the larger islands.

## Climate and Weather

In general, the climate in the Falklands, tempered by the sea, is remarkably equable the year round. The mean annual temperature is 43° F with an annual average of only 12° between the coldest month — July, 37° average — and the warmest month — January, 49° average. The temperature owes its persistent coolness to the cold, deep ocean current that flows northward past the islands from its eastward course around Cape Horn, South America.

Characteristic of the year-round weather are the almost incessant winds, primarily the great westerlies. Their prevailing direction is actually from the northwest, but they also come frequently from the west and southwest and even from the north. Winds from any other direction are unusual. There appears to be no marked correlation between wind direction and season. Summer or winter, the direction is the same although during the winter the percentage of south winds increases slightly, yet never enough to have an appreciable effect on the average daily temperature.

It is their strength, as much as their incessancy and westerly direction, that makes the winds an important environmental factor. Throughout the year their average velocity is 17 to 18 miles per hour. For more than two-thirds of the time the speed is between 13 and 38 mph, while gales — 39 to 54 mph — occur three percent of the time. Usually the winds come in forceful gusts with intervening, irregular periods of diminished velocities. Although the spring and fall months tend to be windier, gales take place in any month. At night the winds moderate to some extent but have the same unsteady character.

Rainfall averages 26 inches per year. Though the summer months are

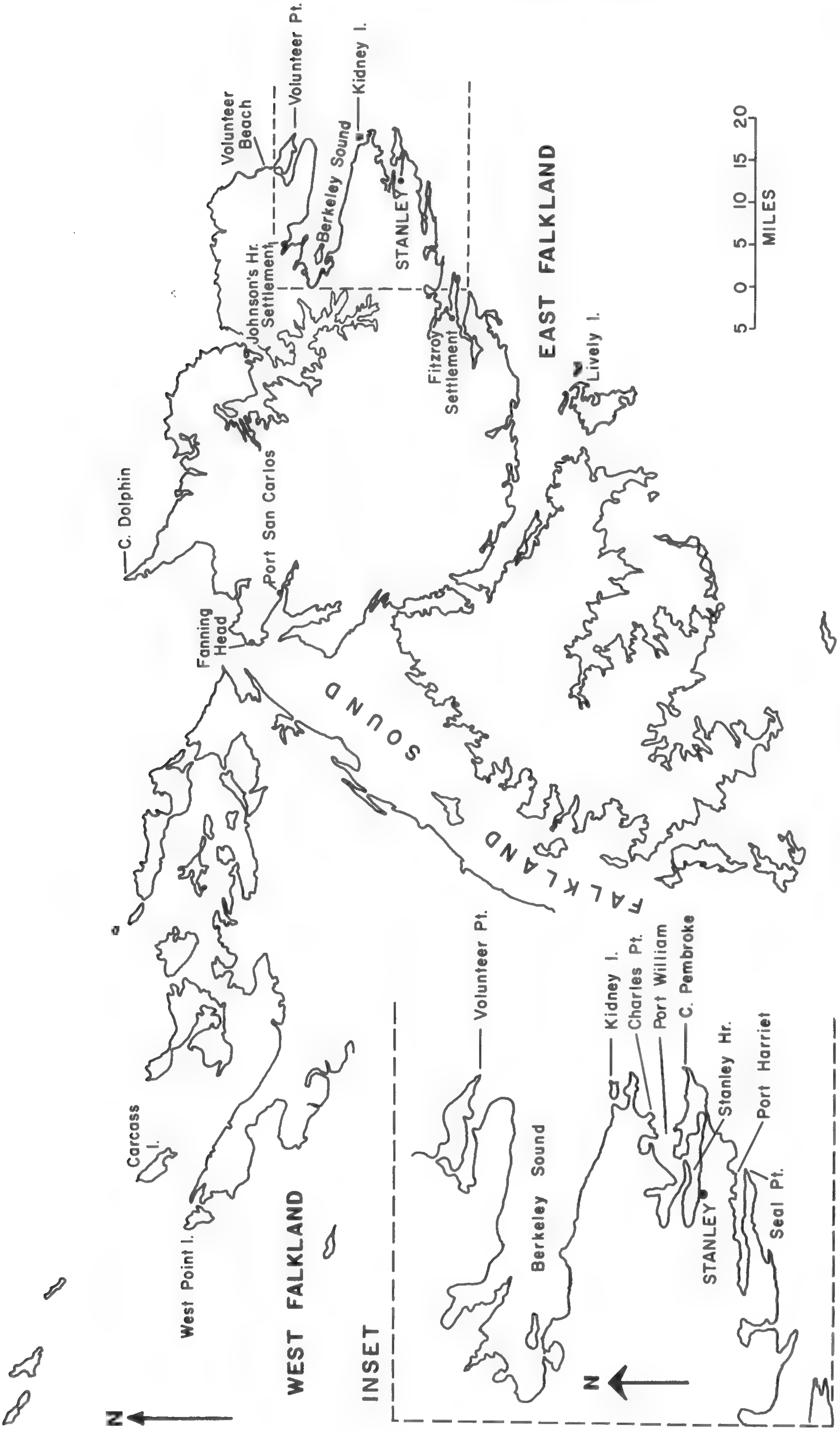
Volunteer Beach
Volunteer Pt.
Kidney I.
Berkeley Sound
Johnson's Hr. Settlement
STANLEY
EAST FALKLAND
Fitzroy Settlement
Lively I.
C. Dolphin
Port San Carlos
Fanning Head
FALKLAND SOUND
Carcass I.
West Point I.
WEST FALKLAND
N
5 0 5 10 15 20
MILES
INSET
Volunteer Pt.
Berkeley Sound
Kidney I.
Charles Pt.
Port William
C. Pembroke
Stanley Hr.
Port Harriet
Seal Pt.
STANLEY
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Figure 1. Map of the Falkland Islands.

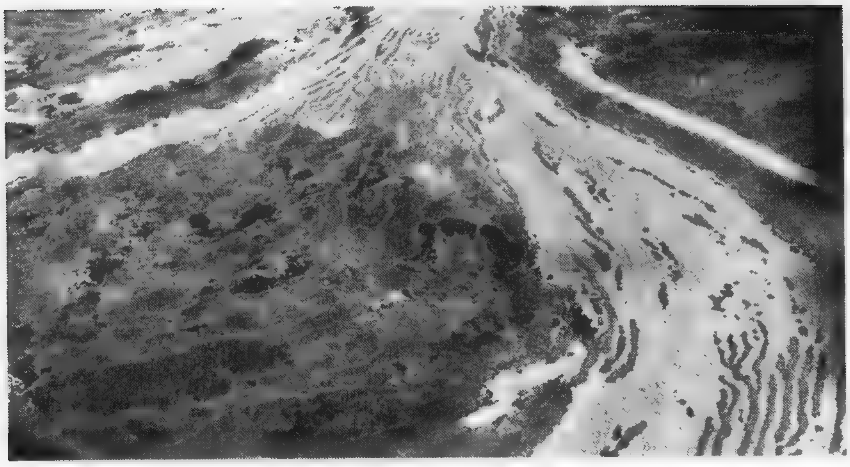


Figure 2. A stone run viewed from the air. Consisting of loose rocks, often of great size, that project from peaty soil on a hillside, the stone run suggests a stream pouring down a slope.

the wettest, there is no month without a considerable share of the precipitation. Hail and sleet occur at least two or three times in every month; and snow falls one or more times in all months except January and February, but seldom stays long on the ground.

The year-round climate is consistently damp, with a daily mean relative humidity of 84 percent. Consequently, there is much cloudiness, but on the average only 60 days a year are completely overcast from dawn to sundown. On other days there are at least brief intervals of sunshine. Totally cloudless days are, however, very rare. In some years there may be several; in others, none.

## Human Settlement and Industry

During the 18th Century, the Falklands were primarily an outpost, a stopping place for sealers and whalers from several nations. Since early in the 19th Century, the islands have been a colony of Great Britain, occupied by English-speaking people, nearly all British or of British descent, whose principal industry is the raising of sheep for the production of wool. During the last forty years the human population has stabilized at approximately 2,300. About half this number live in Stanley, the government center and only town, on the south shore of Stanley Harbour, East Falkland; the other half live in about 30 different settlements widely dispersed on either the two main islands or the larger outlying islands, usually at the heads of snug harbors and inlets well sheltered from the sea.

Each settlement, ordinarily consisting of three or four farm homes, a woolshed, and paddocks, constitutes the headquarters of one farm (Figure 4), sometimes as small as 10,000 acres, but often larger than 100,000 acres, where sheep graze the year round. Except in the late spring when they are gathered at the settlement for shearing, the sheep roam freely. The farm is also a pasture for a much smaller number of cattle, which provide dairy and meat products for the settlement, and horses for shepherding.

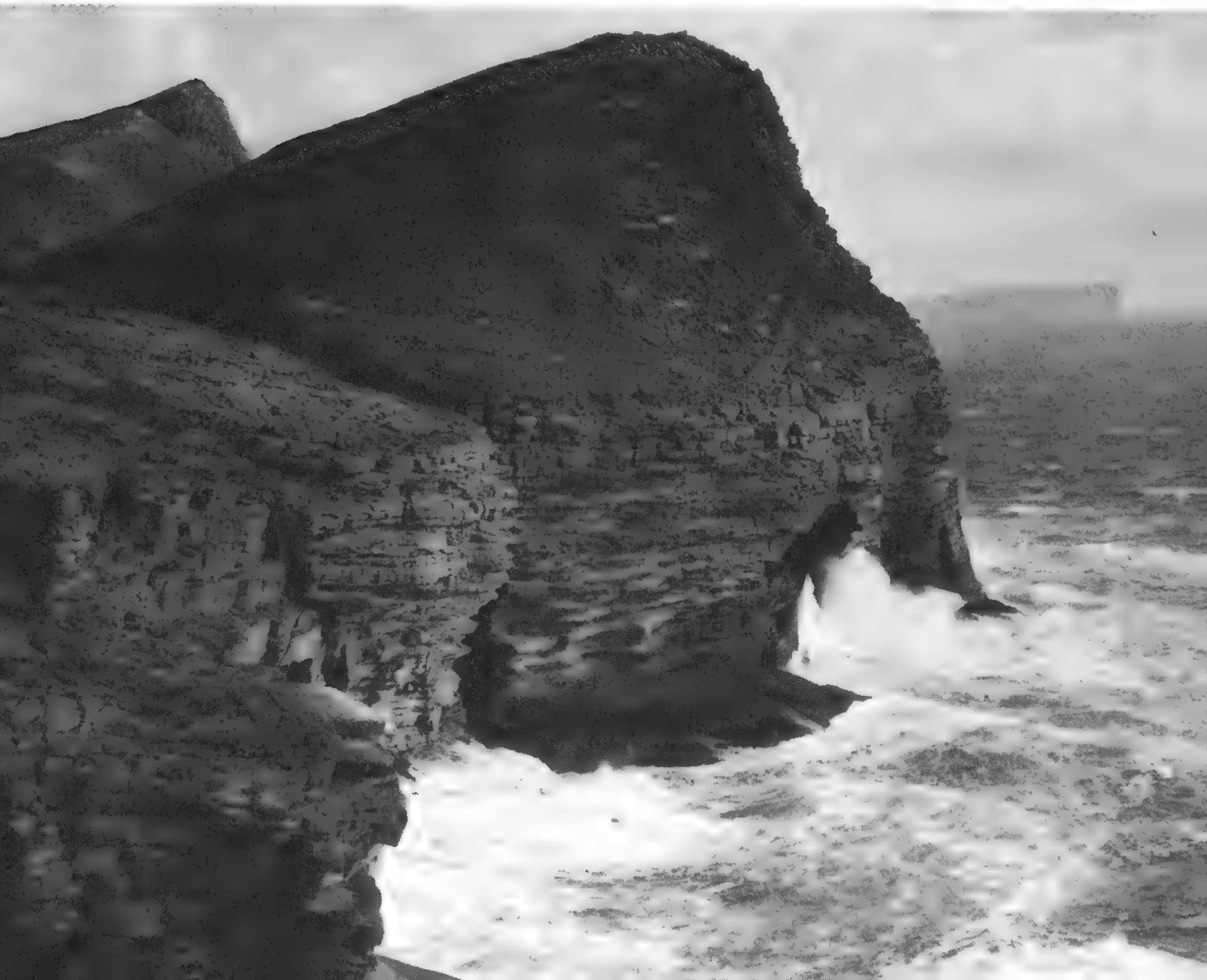
The number of sheep grazed on all the Falkland farms exceeds 600,000 — 635,236 in 1968–1969, according to Davies *et al.* (1971) or about one sheep per 4.5 acres (Richard Cockwell, pers. commun.). This impressive total reflects the singular fact that the Falklands are essentially grasslands, ideal for sheep-farming.

## Vegetation

Except among the stone runs and in the high mountainous areas where lichens and cushion plants (*Azorella, Colobanthus,* etc.) constitute the principal flora, the interior vegetation of the Falklands is dominated by the coarse, clump-forming white grass (*Cortaderia pilosa*), interspersed in the better drained, shaly areas with patches of dwarf shrubs, six to 12 inches high, chiefly diddle-dee (*Empetrum rubrum*). The total aspect is that of a heath (Figure 5). Where the land is poorly drained, white grass and diddle-dee give way to brown rush (*Rostkovia magellanica*), forming, if the ground remains regularly saturated, a true marsh association. Because the blades of white grass, each eight to 10 inches, remain in position for a year or more after they die, hiding the newer green growth beneath, they give much of the landscape in any season a creamy white color. This light hue is relieved by the deep purplish green of diddle-dee patches, the dark brown of rush marshes, and the silvery gray of rock outcroppings.

Between the clumps of white grass, and more especially in the moist valleys and on their adjacent damp slopes where clumps are either widely dispersed or absent, grow meadow grasses (*Poa pratensis* and *P. annua*), bents (*Agrostis*), sedges (*Carex*), a small pointed rush (*Juncus scheuchzerioides*), and pigvine (*Gunnera magellanica*) — plants that are finer than

Figure 3. The bluffs and cliffs of New Island overlooking the open Atlantic. Inland from the bluffs the terrain descends gradually, terminating in beaches on the opposite side of the island.



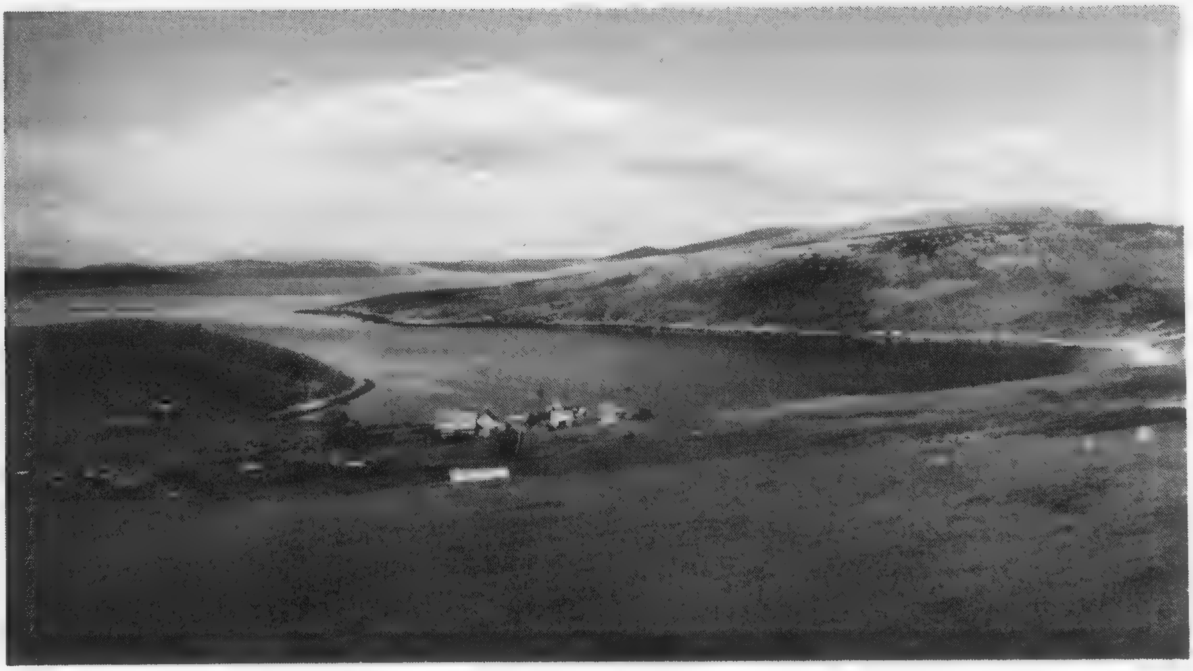


Figure 4. The settlement at West Point Island, one of some 30 settlements in the Falklands, where buildings, tree and shrub plantations, gardens, and domestic animals commonly attract at least five of the nine native passerine birds.

white grass and conspicuously green. In some valleys or near the coasts in the vicinity of penguin colonies, the swards are so dominated by these green plants as to form "greens" which give further relief to the white grass-dominated landscape.

Aside from the dwarf shrubs, the only woody growth indigenous to the Falklands are two bushes that sometimes attain heights of five to seven feet. One is fachine (*Chiliotrichum diffusum*), commonly near valley streams; the other is box (*Veronica* [=*Hebe*] *elliptica*), confined to West Falkland and its larger outlying islands where formerly it was widespread but now, due to overgrazing, restricted to inaccessible cliffs and ravines.

In Stanley and most of the settlements there are a few trees, all introduced, since there are no trees native to the Falklands. The one species that prospers well enough to be of significance is the macrocarpa, or Monterey cypress (*Cupressus macrocarpa*), a thickly foliaged evergreen. Behind Government House in Stanley, a few comprise a small grove known as Government Forest. Planted many years ago, some of the trees are today as high as 25 feet. Elsewhere in Stanley and in the settlements, many macrocarpas have been planted close together around homes where they serve as effective shelters from the wind.

Also in Stanley and most of the settlements is gorse (*Ulex europaeus*), an introduced thorny shrub that reaches a height of six to eight feet. Tending to form dense, practically impenetrable thickets, it is used extensively for hedgerows, shelter belts, and even fences for paddocks.

Fringing the few coasts of East and West Falkland and the larger outlying islands that are inaccessible to livestock, and covering entirely many of the smaller islands not grazed by livestock, is tussock grass (*Poa flabellata*), a most unusual plant and highly important in the ecology of at least four of the nine passerine birds.

Tussock grass (Figure 6) has blades averaging three feet long that spread out and droop over massive bases or pedestals sometimes four to six feet high. In a favorable situation the fully mature tussock clump, its pedestal plus its crown of blades, may range from eight to 12 feet high, occasionally even higher. Each pedestal (Figure 7), in which the blades are rooted, consists of dead and decaying blades overlying a body of peat soil built up from countless earlier generations of blade stems and roots.

On a typical tussock island — an island covered with tussock grass — the clumps of grass, always luxuriant and green the year round, frequently stand so close to one another that their blades interlace, thus forming a canopy. Beneath it exists a network of tunnel-like passages, protected from the winds and bad weather.

## Animal Life

Insects in the Falklands are sharply restricted in variety, especially flying forms, due no doubt to the persisting strength of the winds. There are no dragonflies, damselflies, mayflies, neuropterans, hemipterans, and homopterans. One butterfly and a few moths are the only lepidopterans; one or two ichneumon flies and several parasitic wasps are the only hymenopterans. Honeybees, introduced several times in the past, failed to survive. Dipterans are represented by a few small flies and a blue-bottle fly (*Calliphora*) and coleopterans by several snout beetles and ground beetles, two or three carrion beetles, and a diving beetle (*Dytiscus*). A flightless camel-cricket (*Parudenus*) is common in areas of tussock grass.

Spiders of several varieties occur in tussock grass and shrubs, particularly gorse. Amphipods and insect larvae abound in kelp and seaweed, washed up and decaying on the beach, and tiny shrimps and other small crustaceans are common on beaches at receding and low tides. In the vicinity of settlements, earthworms are numerous in soils that have been enriched by cultivation or livestock.

There are no reptiles in the Falklands and no native land mammals still in existence. The only mammalian predators on passerine birds are human symbionts, notably cats, which are feral on some islands, and probably rats and mice.

Fifty-seven species of birds regularly breed in the Falklands. This number includes the introduced House Sparrow (*Passer domesticus*), well estab-

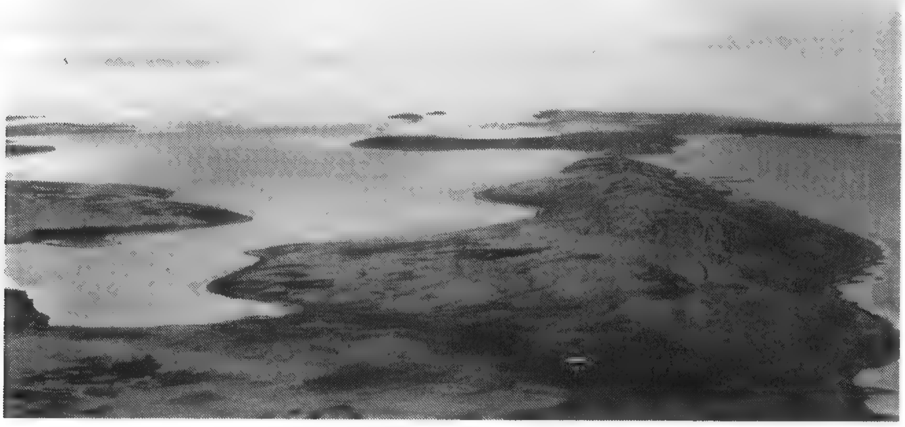


Figure 5. The interior vegetation of the Falklands gives the aspect of a heath, dominated by white grass interspersed with dark-colored patches of either dwarf shrubs, chiefly diddle-dee, or brown rushes. The white grass and diddle-dee heath is the most extensive area in both East and West Falkland and the natural habitat of three passerine birds.

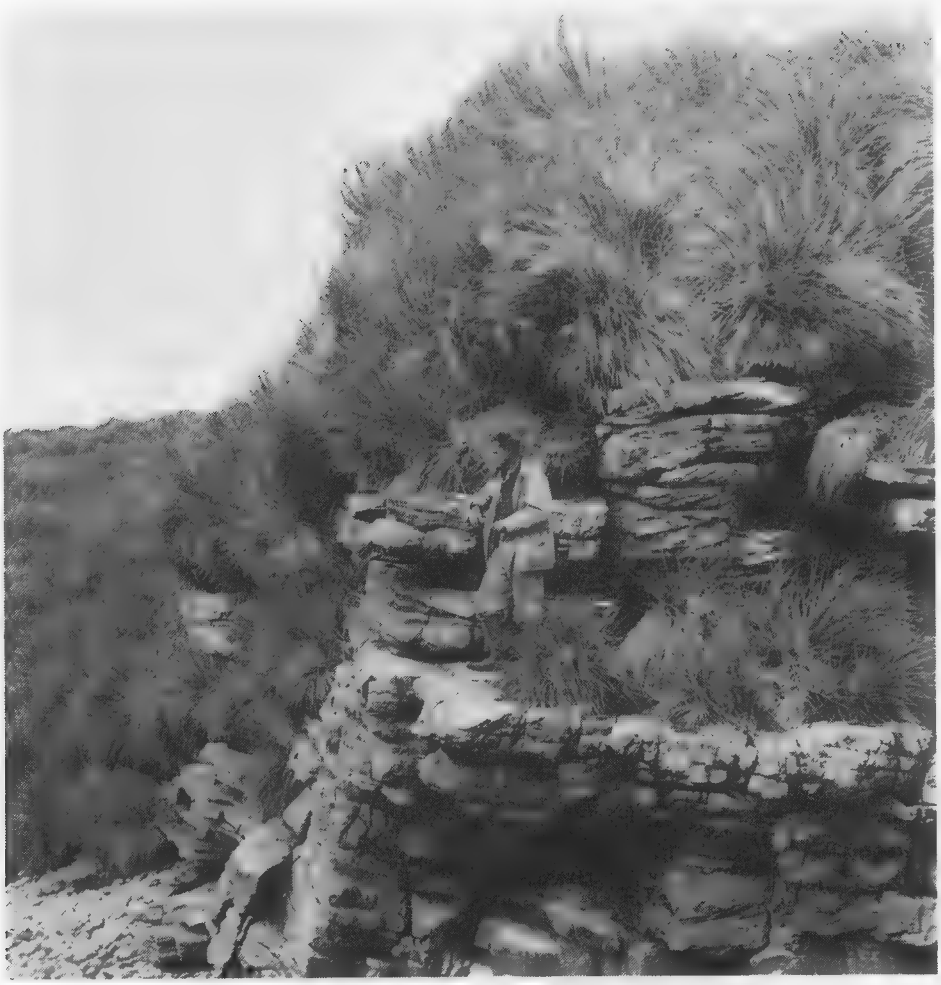


Figure 6. Tussock grass, fringing the coasts of the larger islands and covering many of the smaller islands not grazed by livestock, comprises an important habitat of at least four passerine birds. Photograph by Eleanor R. Pettingill.

lished in Stanley and several of the settlements, and the Peregrine Falcon (*Falco peregrinus*), Red-backed Hawk (*Buteo polyosoma*), and Short-eared Owl (*Asio flammeus*) — the three species of predators most likely to take passerine birds.

## *Itinerary and Observation Areas*

Mrs. Pettingill and I arrived in the Falklands on 22 October 1953 and departed 9 March 1954. We did not return, except for a three-day visit during which time we made no important observations on passerine birds, until 1971 when, accompanied by Maurice A. E. Rumboll, we arrived on 8 November and departed on 24 March 1972.

The areas where we made our observations and the dates we worked in them are as follows:

*Stanley and Immediate Vicinity:* 24–27 October, 13–27 November, 6, 11, 22–28 December 1953; 3, 7 March 1954; 25–29 November, 22–28 December 1971; 25 February–23 March 1972. Principal observations on the outskirts of Stanley, Sappers Hill, Stanley Commons, York Bay, Moody Valley, Murrel Creek, and Cape Pembroke.

*Charles Point* and *Arrow Point*, adjacent peninsulas jutting south into Port William, northeast of Stanley: 28 October–1 November, 7–10 December 1953; 3–9 February 1954.

*Kidney Island*, northeast of Stanley and Port William: 3–7 November, 28 November–5 December 1953; 12–26 February 1954; 10–23 November 1971; 12–19 February 1972. A typical tussock island with the additional features of a sheltered beach, partly sand, partly boulder-strewn, on one side and cliffs on the ocean side that attract a colony of Rockhopper Penguins (*Eudyptes crestatus*) and King Cormorants (*Phalacrocorax albiventer*). Over the interior of the island were nesting burrows of the Magellanic Penguin

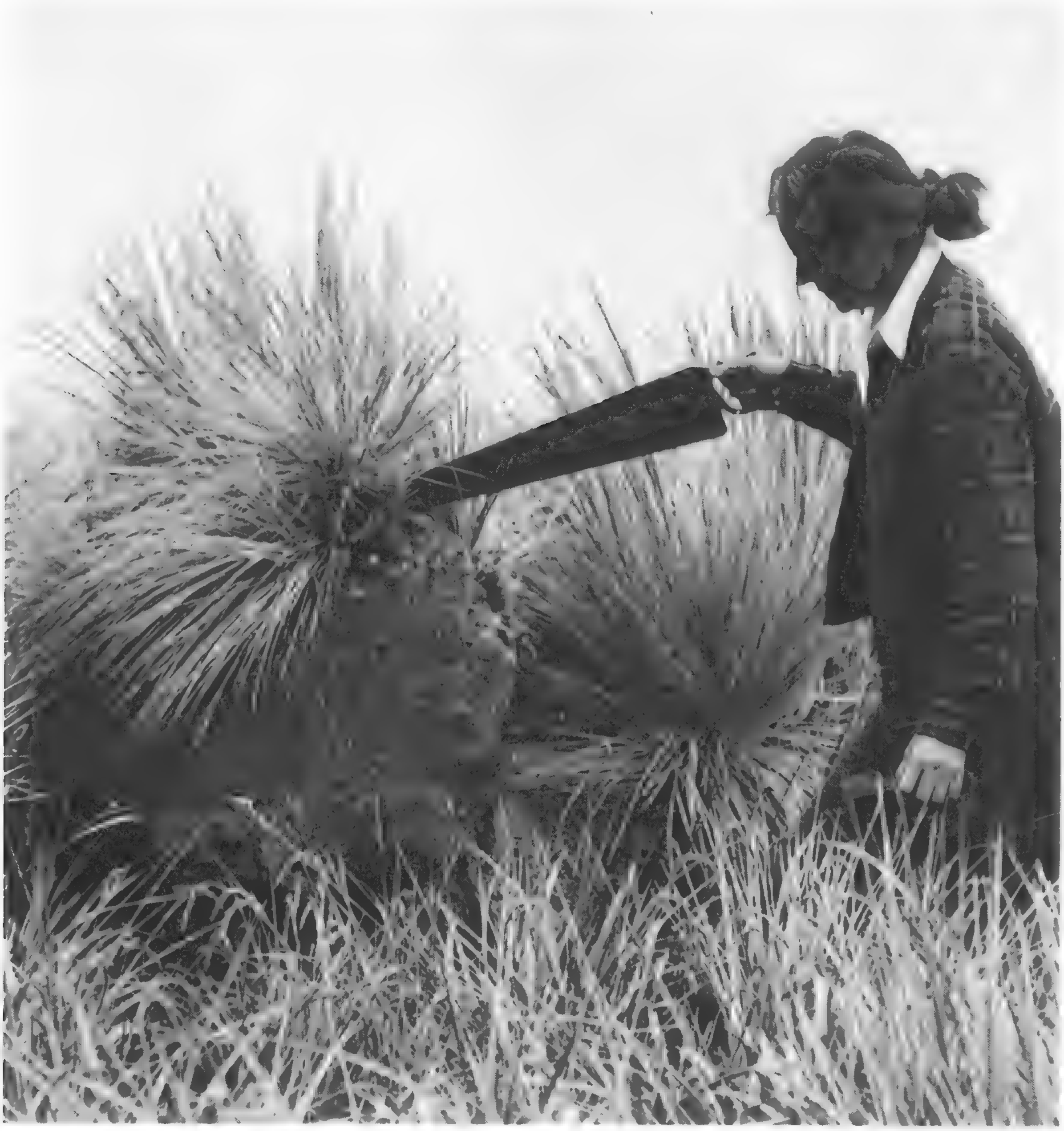


Figure 7. A comparatively small clump of tussock grass with one side sawed off to show the size, height, and shape of its pedestal of peaty soil. Clumps of tussock grass frequently stand so close together that their blades interlace, forming a canopy.

(*Spheniscus magellanicus*), White-chinned Petrel (*Procellaria aequinoctialis*), Sooty Shearwater (*Puffinus griseus*), Gray-backed Storm Petrel (*Garrodia nereis*), and Subantarctic Diving Petrel (*Pelecanoides urinatrix*). See Woods (1970) for an excellent paper on the avian ecology of the island.

*Carcass Island*, northwest off West Falkland: 18 December 1953.

*New Island*, west off West Falkland: 29 December 1953–30 January 1954; 29 December 1971–18 January 1972.

*Volunteer Beach*, extreme northeast East Falkland, between Cow Bay and Volunteer Point: 30 November–5 December 1971; 1–7 February 1972. Extensive greens and white grass-dwarf shrub associations inland from the beach.

*Port San Carlos Farm*, extreme northeast East Falkland, including Fanning Island, Fanning Head, and Cape Dolphin: 6–12 December 1971.

*West Point Island*, northwest off West Falkland: 18 December 1953; 12–21 December 1971.

*Fox Bay East Farm*, east West Falkland, including Carcass Bay: 19–23 January 1972.

*Seal Point*, south of Stanley and Port Harriet: 10 February 1972.

*Fitzroy Settlement*, east East Falkland, including Cow Point: 24–25 February 1972.

## *Species Accounts*

### TUSSOCKBIRD

(Figures 8 and 9)

*Status.* — Common resident on certain of the smaller islands with abundant tussock grass. Nesting season: September through early January.

*Observations.* — This species, belonging to the South American family Furnariidae and occurring in the vicinity of Cape Horn and the Beagle Channel as well as in the Falklands, is aptly called Tussockbird in the Falklands because of its apparent preference for tussock grass on the outlying islands.

We found Tussockbirds the most abundant species on the beach at Kidney Island. Both sexes were uniformly dark brown, without the more distinctive markings that identify the seven other species of the genus. They walked, sometimes hopped, and flew strongly in a usually direct, rather than undulating, flight. Although plain in their general appearance, Tussockbirds invariably drew our attention by their peculiar actions and extraordinary tameness.

For food, the Tussockbirds relied frequently on the crustaceans, amphipods, insects, and other small arthropods associated with the rows of decaying kelp and seaweed that had washed up on the beach. Often, in order to obtain such food in these soggy heaps, they pecked deep holes, vigorously tugging at, pulling out, and flinging aside tough strands that blocked their excavations. Once they had started holes, it was not unusual for Austral Thrushes, larger and stronger birds, to come along and usurp the holes for their own foraging. This sometimes proved advantageous to the Tussockbirds: after staying close by while the thrushes deepened the holes, obtained their fill of food, and departed, the Tussockbirds soon had more productive holes than they could have made themselves.

The Tussockbirds were not only fearless of us, they were attracted to us! This was puzzling, indeed, until we discovered that our walking over the plant debris stirred up or otherwise dislodged crustaceans and insects, thereby making them more available. The birds, several at a time, followed us at our heels. When we stopped, they walked around and over our feet. When we proceeded to kick over pieces of kelp and seaweed, in no time at all as many as a half dozen birds converged at our feet. In their anxiety, some of the birds arriving on the wing attempted to alight on us and one actually perched momentarily on my shoulder. If we sat still, held out an insect in our hand, and waited awhile, a Tussockbird was almost certain to take it.

Tussockbirds also sought food on the kelp beds offshore, jumping from one floating strand to another. Once, on a calm day when dipterid flies were swarming low above the beach, Tussockbirds kept jumping in the air and catching them with moderate success. Occasionally, Tussockbirds foraged on the sand beach, picking up very tiny red shrimps left on the sand by each receding wave. In the Rockhopper Penguin-King Cormorant colony, Tussockbirds scurried about picking up food — presumably insects and their larvae, spiders, and other arthropodal forms — from the edges of the nests and in the accumulations of excrement. Reynolds (1953:73) described similar foraging by the species in a colony of Rock Cormorants

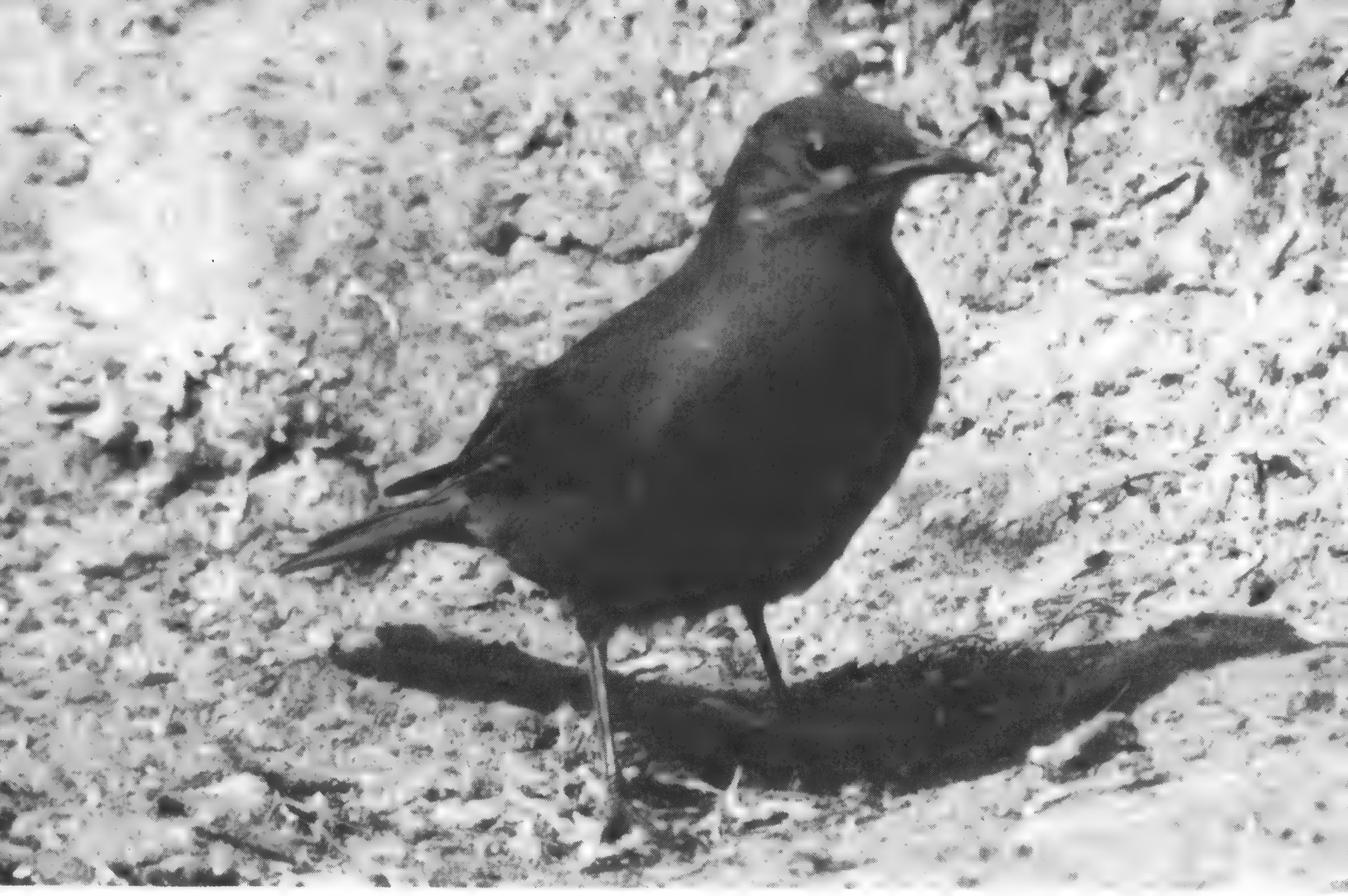


Figure 8. A Tussockbird, interrupted while foraging in a penguin colony on Carcass Island, is instantly alert — probably watching the boots of the photographer and ready to snatch any live food their movement might uncover.

(*Phalacrocorax magellanicus*) in the vicinity of Cape Horn. In the Kidney Island colony they always approached the nests cautiously, staying out of reach of the occupants, which threatened them with open bills if they came too close. Given the opportunity, Tussockbirds ate the contents of broken penguin and cormorant eggs and any food that adult penguins and cormorants regurgitated inadvertently or the young birds vomited on the ground.

We readily attracted Tussockbirds, sometimes two and three at a time, to the vicinity of our hut on Kidney Island by putting bread crumbs and crusts and other scraps of food on a board. Practically anything edible the birds devoured with gusto. To cope with a large crust of bread, they held it down with one foot in order to break off small pieces.

When I put down my camera case and tripod most anywhere on the beach or the edge of the penguin-cormorant colony, it was not long before one or two Tussockbirds were walking around and over them on a tour of inspection.

Nest-building was still in progress when we arrived at Kidney Island on 3 November 1953. I watched several Tussockbirds gathering pieces of dead tussock grass and disappearing with them under loose rocks, or in holes in or under the tussock clumps fringing the beach. I soon realized that this margin of the island's tussock cover, not the interior, provided the habitat for nesting. The birds nested in or under the tussock clumps, not in the crown of tussock blades. Murphy (1936:789) reported Tussockbirds nesting in the burrow of a diving petrel (*Pelecanoides urinatrix*). Cobb (1933:17) found a nest on a beach in an old box 20 inches square that had two entrances.

Tussockbirds were noticeably territorial. By November, the various pairs had already staked out their breeding areas rather evenly along the margin of the tussock grass and defended them jealously, with frequent squabbles. When one bird intruded upon another's domain, it was threatened by wings spread out and lifted above the back, tail spread and elevated, mouth open, and several *chittering* sounds.

Most vocalizations were limited to chittering sounds. A series of such sounds —for example, *chit, chit, chit, chit, chit, chitter, chitter, ee, ee, ee* — I assumed to be a territorial song, because the bird gave it while lifting and waving its wings above its back. More often than not, the songster performed on the beach without ascending ot a sepcial perch. In flight, while walking, or when chasing another individual, a Tussockbird uttered similar sounds, though much more abbreviated.

Occasionally, a Tussockbird also performed a modest flight song, ascending a few feet off the ground, then moving the wings stiffly or somewhat butterfly-like while uttering a few sharp *kick* sounds before descending with wings held high.

When we returned to Kidney Island on 28 November, some of the Tussockbirds were carrying food for young into places where before they had been taking nesting material. With food in their bills, they flew to their nests with great speed, landing, folding their wings, and disappearing, all in an instant. Entrances to their holes were now clearly evident from the white smears of the young birds' droppings which the parents deposited as they emerged after taking in food. Why they did not carry the fecal matter farther away from the nests, as is the case with most passerine birds, I failed to understand. Though we stayed on Kidney Island as late as 5 December, we saw no young out of the nests.

In 1971, we found three nests, one on 14 November under the floor in the shed adjacent to the hut, the second on 18 November under a large boulder on the beach, and the third on 20 November in a tussock clump.

The nest under the floor, easily viewed by lifting up a board, contained three eggs. From the date we found it until 23 November, when we left the island, both adults attended the nest. They followed a routine that

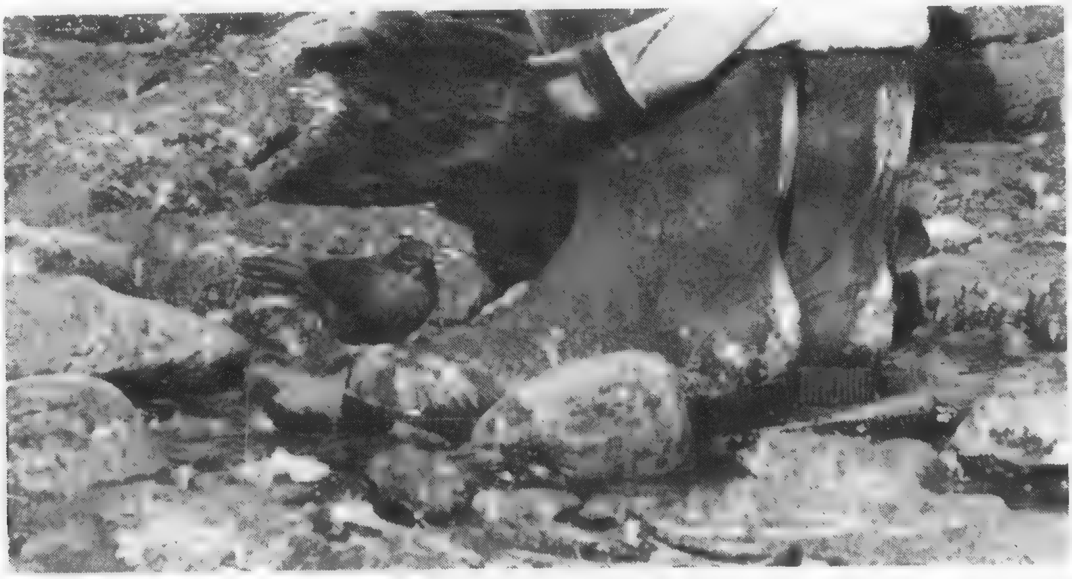


Figure 9. A Tussockbird standing beside the boot of a person pausing on the beach at Kidney Island. Tussockbirds follow anything that moves, be it a boot, sea lion, or penguin, aware that it might dislodge some stones or bits of rotting kelp, revealing food.

consisted of one bird arriving with a few small blades of dead grass for the nest or its entrance path, and taking over incubation for the mate which departed. On one occasion, a bird arrived with a single blade of grass 15 inches long and left it as additional covering for the path. The nest under the boulder, easily viewed from outside, contained two nestlings, five to six days old; their gapes were conspicuously yellow, and darkly colored down grew from all their upper feather tracts. Both adults fed the nestlings. Once, an adult arrived with grass for the nest instead of food for the young. At another time, an adult brought a white feather which its mate removed along with a fecal sac. The nest in the tussock pedestal was at the end of an 18-inch burrow, possibly an old petrel burrow, that entered in the side under a "skirt" of dead tussock blades. We discovered the nest, with two eggs, by seeing the adults carrying in grasses.

We learned, from our observations on the behavior of the adults at the three nests, that carrying materials to the nest continues through most of the nesting cycle and is, therefore, no indication that nesting is beginning, as we once thought. I presume that the habit is a means of keeping the nests dry.

Robin Woods (pers. commun.) noted Tussockbirds at Kidney Island carrying nesting material as early as 30 October 1962 and still feeding unfledged young as late as 3 January 1959. He found five occupied, or recently occupied, nests in natural situations: one under rocks high up on a beach; one five feet into a crevice between upright slabs of rock; one on a flat rock deep under a tussock clump; one about two feet under loose rocks at the base of a cliff; and one at the end of a short tunnel in a peat bank. Interestingly, in 1958, 1959, and 1961, he also found an occupied nest in the same shed, under the floor, where we found a nest in 1971. All the nests that Woods examined were constructed mainly of dead grasses and/or root fibers and two contained a few feathers. Among the food items that he observed being carried to young were camel-crickets and small fish, presumably regurgitated by cormorants in the adjacent colony. He noticed one instance of an adult carrying a fecal sac several yards from the nest before dropping it.

On our trip around the Falklands in mid-December 1953, we were astonished one day, 12 December, to see an adult Tussockbird come aboard our ship, the *R. M. S. Fitzroy,* while anchored off Lively Island. The bird proceeded to forage for insects on the deck, walking about among the hawsers and winches as much at home as if it were on a beach. Ashore at the settlement on Carcass Island, 18 December, I was nearly as astonished to note many birds around the buildings where there was no tussock grass in the immediate vicinity (tussock grass once grew in the area before it was cleared). We noted several fledged young, their tails about full length, begging food from their parents. One youngster, begging food from an adult that was evidently not a parent, was viciously attacked by the adult and took refuge in a nearby rock crevice.

Our hosts told us that the Tussockbirds nested under the buildings and in any wall-crevice they could get into. We watched them come through the windows into the house and take food from the table when we had tea. The food on the floor for the one and only cat was kept covered, except when the cat wanted it, lest it be devoured by the voracious intruders.

The principal reason for the abundance and tameness of Tussockbirds at Carcass Island is that the owners had maintained their island domain as a sanctuary, allowing no cats to roam at random and preventing rats from becoming established. The species had thus been able to survive in an area devoid of its normally tussock-fringed habitat.

This situation at Carcass Island was in sharp contrast to New Island where the settlement was overrun with cats. The only Tussockbirds we saw there were a mile from the settlement in the penguin colony bordered by tussock grass.

In this colony at New Island on 19 January 1954, I watched a pair of Tussockbirds taking food to young in the adjacent cliffs. One might deduce from this remarkably late date that the species has two broods a year, but I believe, as did Cawkell and Hamilton (1961:22), that there is only one brood. The late date was due to some individuals starting to nest later than others and to a long nesting cycle of about 60 days. Cawkell and Hamilton (*loc. cit.*) reported, for example, some careful observations on a nest which covered a period from 8 October, the first day of nest-building, through an incubation period of about 16 days and nestling period of about 25 days, to 8 December, the day of fledging.

At Kidney Island in February 1954 and 1972, the adult Tussockbirds were in various stages of molt. Like the House Wrens, the young birds-of-the-year were in a fresh plumage that was more richly brown and thus readily recognizable.

If anything, the Tussockbirds were more numerous than before. They were just as active on the beach and just as tame. They were also just as quarrelsome, giving their characteristic displays and chitters; but there was no singing.

Woods (pers. commun.) obtained some evidence that Tussockbirds hold territories long after the breeding season, perhaps the year round. One color-banded individual that he saw feeding young at a nest on Kidney Island, 22 November 1961, was in exactly the same place on 16 April 1962. He has records indicating the attachment of Tussockbirds to the same place from one breeding season to the next.

Where, on our earlier visits in November, there had been only a few Tussockbirds about our hut, we saw as many as 15 in February. On putting out food, we attracted Tussockbirds immediately, sometimes six at a time. Before long they were entering the hut by the door, walking over the floor, and flying up on our table. When we closed the door, they tried to enter through the window panes. Their audacity and persistence in searching for food — anything edible — seemed practically boundless.

*Remarks.* — The genus *Cinclodes*, comprising eight species that range in South America from the high Andes of Venezuela and Ecuador south to Tierra del Fuego and Cape Horn, evidently prefers the vicinity of water, whether it is a mountain stream or the sea. Besides the Blackish Cinclodes, at least one other species in the genus, the Seaside Cinclodes (*nigrofumosus*), occurs only on the coast. Two other cinclodes, the Dark-bellied (*patagonicus*) and Bar-winged (*fuscus*), regularly occur along the coast, particularly in the southern part of their ranges — for example, in Tierra del Fuego (see Humphrey *et al.*, 1970). All forage at the sea's edge and may, like the Tussockbird, feed offshore on floating kelp when available. Probably no other passerine birds in the world are quite so marine in this respect.

Only in the Falklands, apparently, do the coast-dwelling cinclodes show such marked preference for the vicinity of tussock grass. Reynolds (1935:72–73) wrote that the Blackish Cinclodes breeds in "the more inaccessible places and deep crevices of the rocky coast" and reported a nesting hole in "a steep peaty bank overlooking the sea." References quoted by Humphrey *et al.* (1970) about the nesting of the Dark-bellied and Bar-winged Cinclodes in crevices in cliff walls did not mention tussock grass or any other vegetation; nor did Johnson (1967:164) in describing the nest sites of the Seaside Cinclodes — "inaccessible holes or crevices among the rocks and boulders . . . never away from the coast." As we noted at Carcass Island, the Tussockbird nested away from tussock grass when the circumstances were favorable, but it was exceptional. Although several times at New Island I observed Tussockbirds flying into crevices in the cliffs below the big seabird colony, where I presumed they were nesting, tussock grass was growing on shelves and from crannies nearby.

One may contend that the presence of Tussockbirds in the neighborhood of tussock grass is coincidence since both the birds and the plants are confined to the immediate vicinity of the sea. Against this argument is the fact that outlying islands of the Falkland archipelago without tussock grass have no Tussockbirds, and the observation, alluded to by Cawkell and Hamilton (1961:2), that when tussock grass has been overgrazed by sheep or otherwise virtually destroyed on islands where the Tussockbirds once thrived, the birds eventually vanish.

Johnson (1967:160), in noting the preference of the genus *Cinclodes* for water, also made the generalization that it has a "crouching stance and bobbing characteristic movements" shared with the genus *Cinclus*, the dippers. Wetmore (1926:251–252) reported that Bar-winged Cinclodes "walk on the ground with constantly wagging tails" and that the Gray-flanked Cinclodes (*oustaleti*) had the habit of "constantly wagging the tail" in a manner similar to the waterthrushes (*Seiurus*) of North America. The Tussockbird showed none of these actions and I can find no report of either the Seaside Cinclodes or the Dark-bellied Cinclodes performing them. Possibly the actions are a development only in those species of *Cinclodes* whose primary foraging places are mountain streams and other inland waterways.

When handling Tussockbirds, I was impressed by their musty odor — a peculiarity noted also by Woods (pers. commun.). In the skins of specimens that I collected in 1953–1954, the odor persisted long afterwards. Possibly the odor was acquired from the places in which the birds nested or roosted.

As I have already indicated, Tussockbirds are very tame and notably opportunistic in foraging. Cobb (1933:33) wrote of them coming into woolsheds while sheep-shearing was in progress and hunting for ticks in the fleeces. The extent to which other cinclodes are tame or opportunistic is unknown, but at least the Bar-winged Cinclodes, according to Reynolds (1935:74), is tame enough "to investigate visitors or their camp-kit, and to take advantage of disturbed ground where insects may be taken."

## DARK-FACED GROUND-TYRANT

(Plate I, Figure 10)

*Status.* — Resident, common in stone runs and in valleys with rocky outcroppings, also common on rocky coasts. Nesting season: October through December.

*Observations.* — We encountered this moderately sized, long-legged, predominantly bluish-gray flycatcher in all places that we visited. Its particular habitat seemed to be governed by the availability of crevices in loose rock or ledges for nesting and places sheltered from the wind for feeding and resting.

Our first chance to watch Dark-faced Ground-tyrants for any period of time was at Charles Point from 28 October to 1 November and 7–10 December 1953. The spots where we found them varied with the direction and strength of the wind at a particular time. Thus, if the wind was from the west, we could expect them along the beach in the shelter of the bluffs; if the wind blew onshore, the chances were that they would be inland in deep ravines. On the rare occasions when the wind was slight, we came upon them almost any place. When alighting, they simultaneously flipped their closed wings and spread and dipped their tails. Once perched, they kept their heads high and body noticeably upright.

Many times we observed ground-tyrants catching insects on the ground or on ledges. Typically, the bird left its high vantage point, hovered momentarily, then fluttered and "parachuted" down, tail spread, to land and snap up the insect almost at the same time. Sometimes it stayed on the ground to walk, run, or hop after another. Should the insect be flying or otherwise moving, the bird pursued it with hops and bounce flights. Should the insects be numerous on the spot where the bird made its first capture, it usually stayed and continued foraging for a short while. If the ground was grassy, the bird's long legs were a distinct asset in permitting it to stand high and see its prey at a greater distance.

Robin Woods (pers. commun.) watched two ground-tyrants hovering quite stationary from one to 15 feet above ground as they hunted for small moths in long white grass. On spotting a moth, they dropped rapidly to pick it up, then flew up to move along a few feet to hover again. Woods noted that, when hovering in a strong gusty wind, ground-tyrants held their wings straight out and flapped them in short arcs more below than above the horizontal; they kept the tail well spread and, though they sometimes tilted it, they did not depress it much, if at all.

Only on a few occasions did I notice a ground-tyrant actually hawk an insect in midair, either by a foray from a vantage point or from the ground. Whether this infrequency of the habit, so common in most Tyrannidae, was due to the paucity of flying insects or to a waning of the habit in favor of more productive ground-foraging, is open to speculation. I assume that the species' long legs and its habit of ground-foraging represent an adaptation to a cool, windy environment where the source of insects is principally on or close to the ground.

We noticed ground-tyrants hunting along a stream by taking regular flights down from the embankment to pick up insects at the water's edge.

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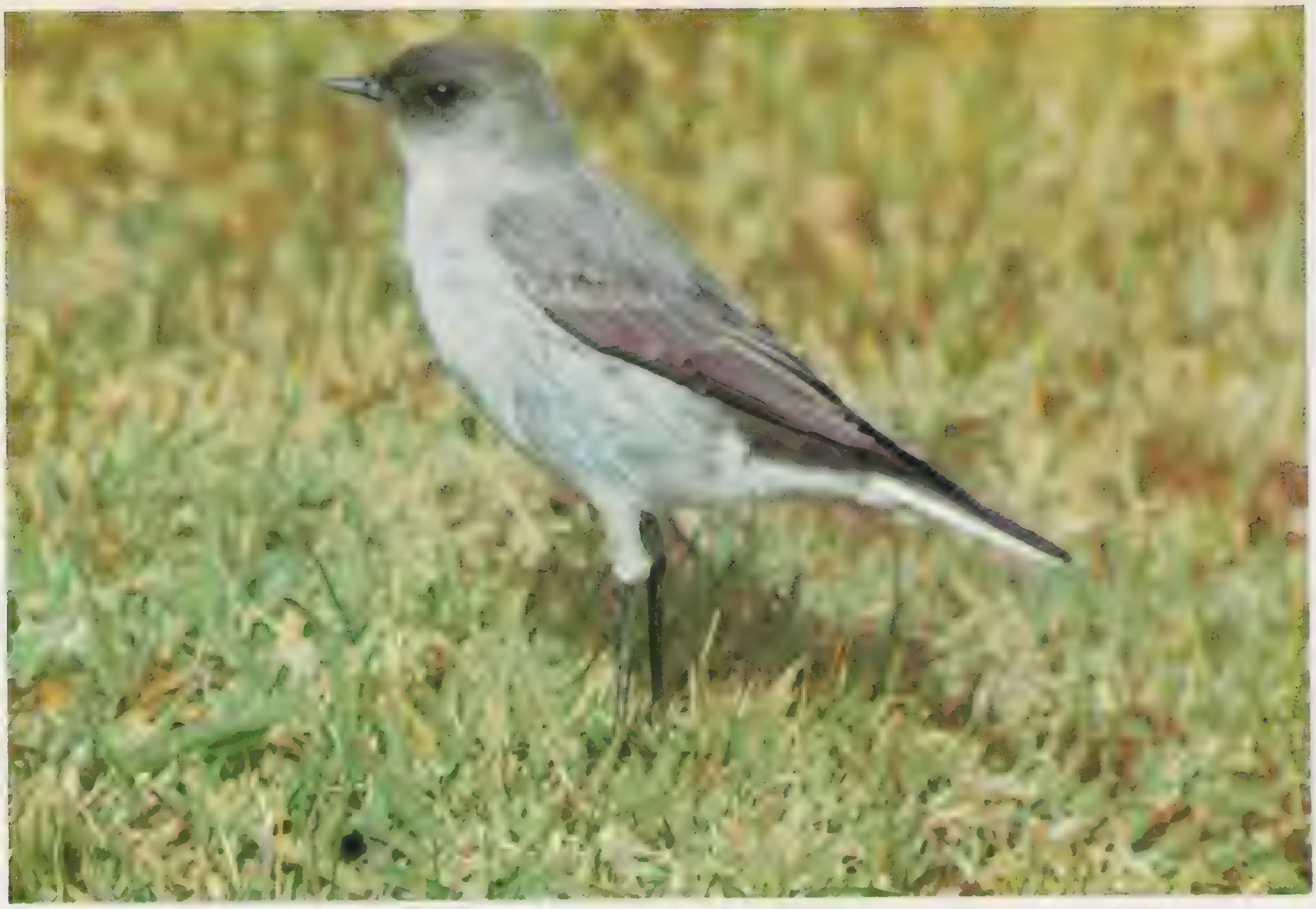
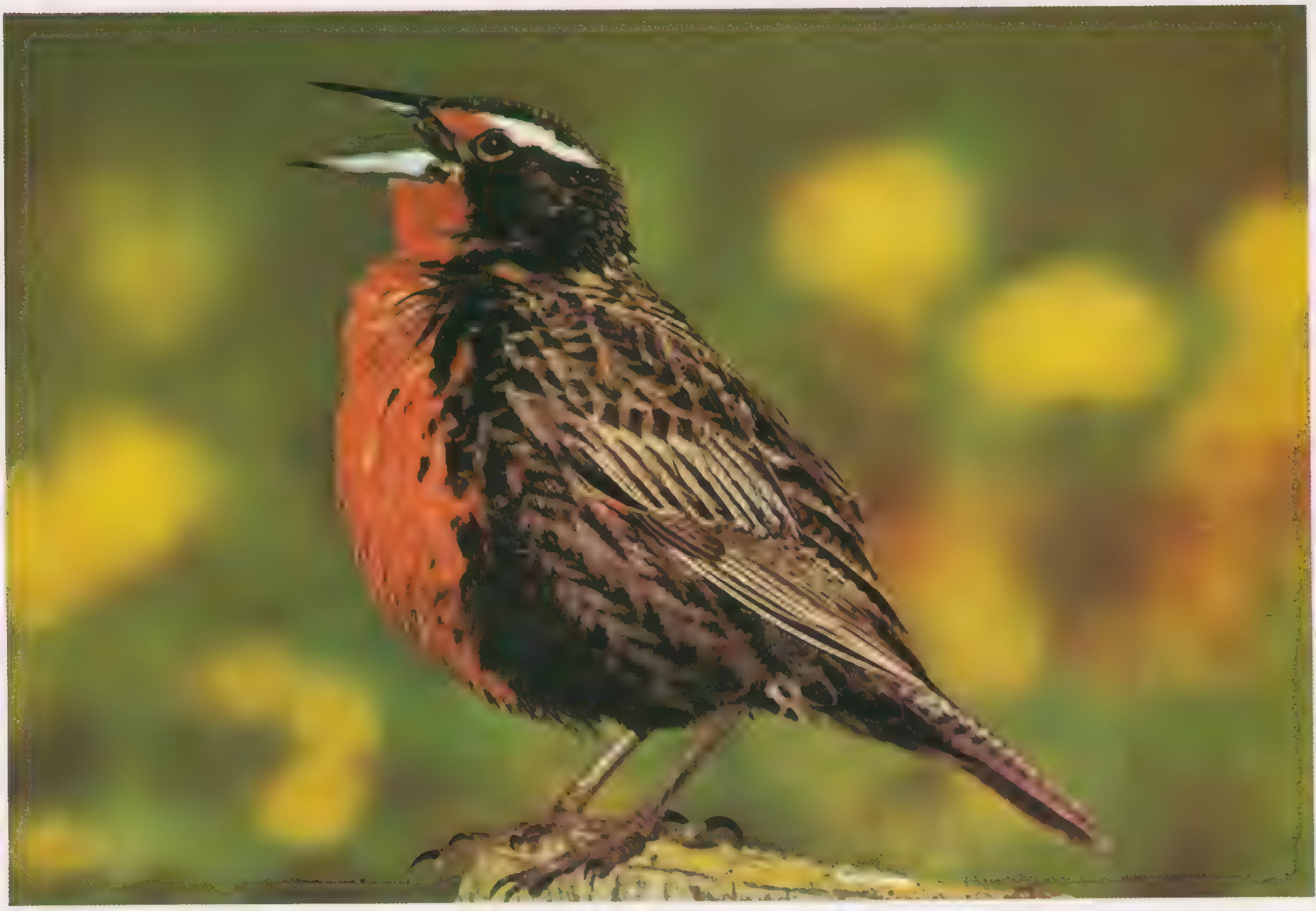
Plate I. *Above,* Dark-faced Ground-tyrant, *Muscisaxicola macloviana.*
*Below,* Long-tailed Meadowlark, *Sturnella loyca.*



*Above,* Dark-faced Ground-tyrant, *Muscisaxicola macloviana.*
*Below,* Long-tailed Meadowlark, *Sturnella loyca.*



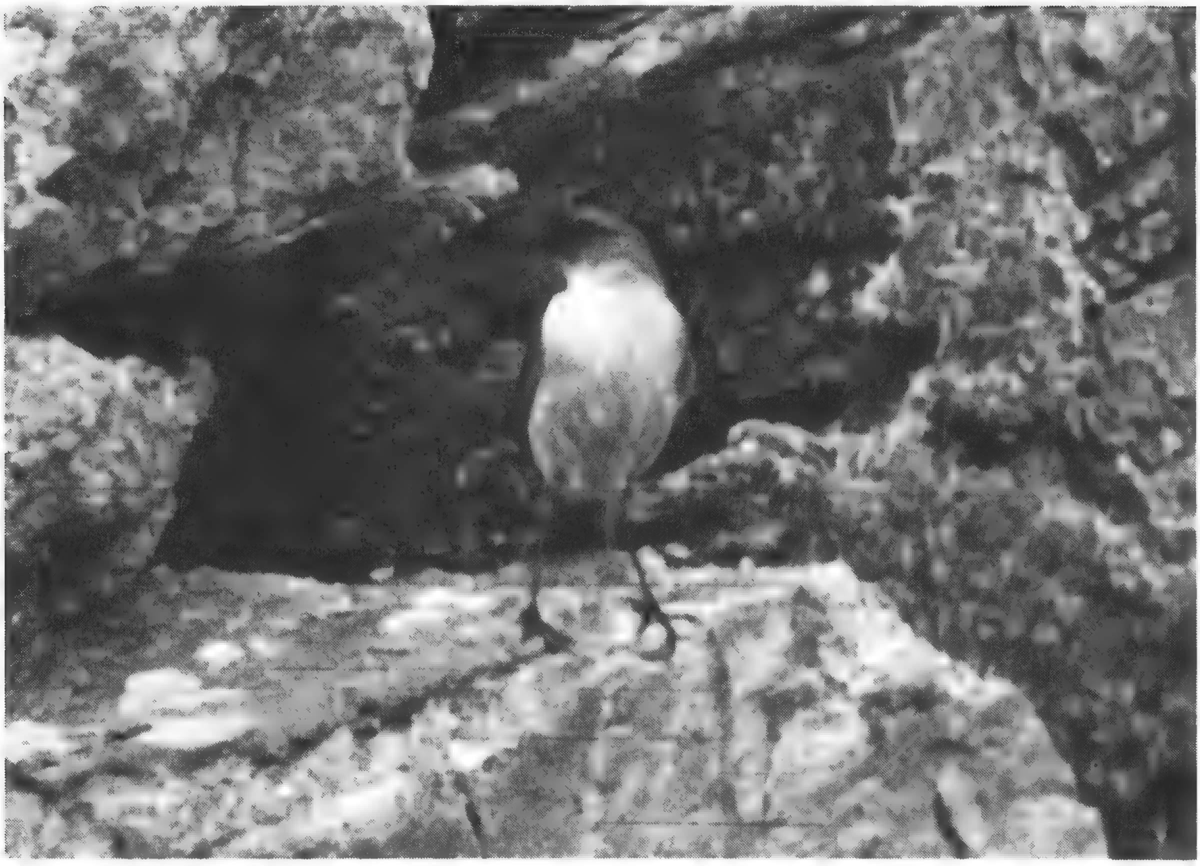


Figure 10. A Dark-faced Ground-tyrant at Charles Point stands in front of the entrance to its nest, the crevice on the left. For a flycatcher, its legs are exceptionally long, an asset which permits the bird to stand high on grassy ground and thus see its prey at a greater distance.

We also watched them foraging on the face of the high cliff at Charles Point itself and visiting the beach at nearby Rabbit Cove to pick insects off the rows of washed up and decaying seaweed and kelp.

Vocally, the ground-tyrants were quiet, their utterances simple and subdued compared to most tyrannids. Their principal call, given when alarmed or when pursuing another bird, was a reedy *cheep* uttered in a rapid series and quite audible, even in a strong wind. Another call, noted by Woods (pers. commun.), was a low, hard *tu,* which may be repeated rapidly and sometimes combined with the *cheep* note — *chee-tu* — with the accent on the *tu.* A protest note, when I handled the bird, was a faint *seep.* Several times I heard a pleasing series of warbling sounds that may have been a territorial song.

Cawkell and Hamilton (1961:22) wrote of a possible display in which a ground-tyrant "flies a few feet into the air and descends with a tumbling flight on to some rock." In October 1959, Woods (pers. commun.) saw a bird flutter up to about 50 feet, then drop down onto a rock. We did not see any such aerial performance, nor did we observe the following performance, obviously a display, which both Stuart Booth and Woods (pers. communs.) described to me: In September 1972, Booth on two different occasions watched a ground-tyrant, while standing before two others, raise its wings high from five to 10 seconds in one position, then move to another position within a yard or two and repeat the performance. During September 1959, Woods noticed two different birds, presumably males, performing in each case before a smaller bird, presumably a female, by raising one or both wings at about 60 degrees above the horizontal. The action reminded him of butterflies sunning themselves, opening and closing their wings slowly. The performances seemed to be emphasizing the pale, slightly shiny underside of the wings and the darker patch of feathers on the flanks. In all respects these descriptions by Booth and Woods conform to the display called Wing Raising by W. J. Smith (*in* Smith and Vuilleumier, 1971), who observed and described it in agonistic encounters of several other species of *Muscisaxicola* and believed it characteristic of the genus.

On 10 December 1953, I found a pair at Charles Point nesting in a foot-deep crevice of a high ledge (Figure 10). I could not reach the nest, but I could hear the young begging in response to sounds that I made. Both adults brought food which, in a few instances, I recognized as caterpillars and spiders. Brooks (1917:158) wrote of a nest on 27 October 1915 with three newly hatched young "deep down among the rocks." In order to reach it, he had to remove many loose stones. The nest was "quite large and well constructed of grass and moss, the lining being of feathers." He noted that the young were being fed spiders. Cawkell and Hamilton (1961: 22) reported a nest "thickly lined with wool and on top of that chicken feathers." Woods (pers. commun.) found a nest, 29 November 1959, on a ledge in a small cave with only about five inches between the nest and the roof. The nest was constructed of dry grass stems and lined with feathers of other species. On 24 November 1960, he found another nest with two young nearly ready to fledge, close to the edge of a stone run, about two and one-half feet under a large overhanging, half-buried stone. The nest, greatly flattened from long use, was made of plant fibers, mostly grass roots, and lined with feathers of other species. Woods saw both parents, in turn, enter the nest cavity with bills full of moths.

The flight of ground-tyrants, we observed, was fast, often undulating, and strong, enabling them to cover considerable territory, even in the brisker winds. To gather food for the young in the nest on the high ledge at Charles Point, the adults had to fly some 100 feet down to the beach, or to a grassy plot equally far away, and return, sometimes in the face of a gale. On the beach at Kidney Island, an individual appeared now and then, possibly having flown across the narrow channel from East Falkland or from the other side of Kidney Island where it may have been nesting in the cliffs.

During our stays on New Island in late December and January, ground-tyrants were very common about the settlement, although no more numerous elsewhere on the island than they were at Charles Point. The shelter from the wind provided by the buildings, the vantage points for foraging provided by the fence posts around the sheep paddocks, and the abundance of insects for food occasioned by the domestic stock — sheep, cattle, horses, and poultry — made an ideal habitat, albeit man-made. Occasionally a ground-tyrant fluttered about the windows of the main house, attempting to catch flies that it could see on the inside. Because of this trait — coming to the windows and sometimes flying into the house, as though bearing a message — many people in the Falkland settlements call the species the "News Bird."

In January at New Island in both 1954 and 1972, the adult ground-tyrants were in varying stages of molt. The young were, in nearly all cases, full grown and, with the exception of one still being fed by its parents, were completely independent and no longer in family groups.

When a vagrant Fork-tailed Flycatcher (*Muscivora tyrannus*) appeared, 7 January 1972, on a fence bordering the settlement, one or more ground-tyrants perched near the stranger and harassed its every move, including its forays for insects, by taking flight and swooping on it, though never striking. The next day they paid no attention to it. Woods (pers. commun.) reported a vagrant flycatcher, the Fire-eyed Diucon (*Pyrope pyrope*), on the outskirts of Stanley, 10 July 1961, that a ground-tyrant persisted in following until the vagrant finally discouraged the ground-tyrant by chasing it.

Cawkell and Hamilton (1961:22) considered the ground-tyrant a year-round resident. Throughout the winter of 1972, Booth (pers. commun.) saw ground-tyrants in twos or threes around the coast during all his field trips and noted an increase in numbers on headlands. Woods (pers. commun.) found ground-tyrants frequently on the coasts in winter and single birds in the gardens at Stanley where they are not present in the breeding season.

*Remarks.* — In South America, the Dark-faced Ground-tyrant breeds along the Andes from approximately 41° S Lat. southward to Tierra del Fuego (F. Vuilleumier *in* Smith and Vuilleumier, 1971:217). It prefers open, bleak, primarily windswept country — country remarkably similar to the Falklands. Crawshay (1907:64–65), Reynolds (1934:344), and Olrog (1948: 516) emphasized the frequency of the species above timberline in the mountains of Tierra del Fuego; Crawshay remarked that it was "the one living creature" he saw on the bald summit of Nose Peak at 2,225 feet elevation. Crawshay also noted its frequency on flat lowlands bordering the coast.

The Dark-faced Ground-tyrant together with the eleven to twelve other species belonging to its genus were declared by W. J. Smith (*in* Smith and Vuilleumier, 1971), after his thorough study and review of ground-tyrant behavior, to be among the most terrestrial of the entire family Tyrannidae. Besides doing some or much of their foraging on the ground, all the species build open, cupped nests solely on the ground. In the Falklands, the Dark-faced species, if we may judge from the few precise breeding records, situates its nest consistently under rocks or in ledge crevices, always well sheltered from the wind. Probably it chooses similarly protected sites in South America, although, strangely, nobody has yet reported a nest anywhere on the continent.

According to data assembled by Humphrey *et al.* (1970), the Dark-faced Ground-tyrant in Tierra del Fuego is a "breeding visitor" in the summer, arriving from the north beginning in September. In Chile during March and April, there is "a noticeable" movement of the species northward on both sides of the Andes and "an even more evident" return movement between September and October (Johnson, 1967:250). In the Falklands, however, the species apparently remains the year round; many move about the islands, but there is no proof to date that any of the population migrates to or from the archipelago.

## GRASS WREN

(Figure 11)

*Status.* — Common resident on tussock islands and in inland areas where there is a high, thick cover of rushes. Nesting season: October through December.

*Observations.* — At Kidney Island we found the Grass Wren occupying only the tussock-covered interior, particularly around our hut where the tussock grass was interrupted by little areas in which rushes and tall grasses thrived. At no time did it appear on the beach, cliffs, or anywhere else. In all his months of study on Kidney Island, Robin Woods (pers. commun.) saw a Grass Wren just once away from the interior — on the beach where it perched briefly on a dead kelp root before flying back into the tussock grass.

In 1953, several males sang vigorously in pleasant weather throughout our stay from 3 November until 7 November. They were still in song from 28 November to 5 December.

A typical song was a pleasing series of ripples and warbles. It was less explosive than the House Wren's songs, more musical, and frequently descending toward the end. I found it very different from the chattering song of the North American populations of the Grass Wren.

The wrens commonly sang when the weather was sunny and calm, perching in full view, with tail straight up, on tussock blades at the top of the clumps. Frequently they flew, singing continuously with wings whirring, from the top of one clump to another. But when the winds were strong, as was often the case, they stayed deep in the tussock grass and we rarely heard them sing.

We found no nests. According to the description of a typical nest by Cawkell and Hamilton (1961:23), nests are made of grasses and are ball-shaped, apparently like those built by the same species in North America. An entrance at one side leads to a chamber whose base "may have some fine down in it and above this . . . wool . . . and on top some goose feathers."

On 3 December, a family consisting of both adults and at least two fledged young stayed near our hut. They seemed constantly on the move among the tussock clumps, as well as in the thick rushes and grasses where the clumps had long since been cleared. Although we rarely obtained good views of them, we were aware of them nonetheless, because of the persistent singing of the male and their alarm notes — a series of loud rattly chatters, *chup, chup, churrrr; chup, chup, churr.* By squeaking, I was often able to excite them into chattering.

The wrens were around our hut during our stay from 12 to 27 February. This we knew from their now familiar chattering.

During our stays at Kidney Island in November 1971 and February 1972, we found Grass Wrens as common as they had been 18 years earlier and still confined to the interior. Again we found no nests.

Elsewhere in the Falklands during December 1971 we noted Grass Wrens singing among tall rushes and ferns inland from Fanning Head, in tall rushes in a ravine on West Point Island, and in tussock grass in the interior of Fanning Island. Late in January, near Swan Pond not far from Fitzroy Settlement, we came upon a family with young full grown among the rushes and tall grasses. These observations provide strong evidence that the species, unlike the House Wren, is much less restricted in its habitat requirements.

Woods (pers. commun.) observed Grass Wrens singing in the Falklands from early September to early December, with a resurgence in early February. He heard none singing at Kidney Island between 8 and 12 April 1961. His earliest breeding record was a nest with five eggs on 9 October

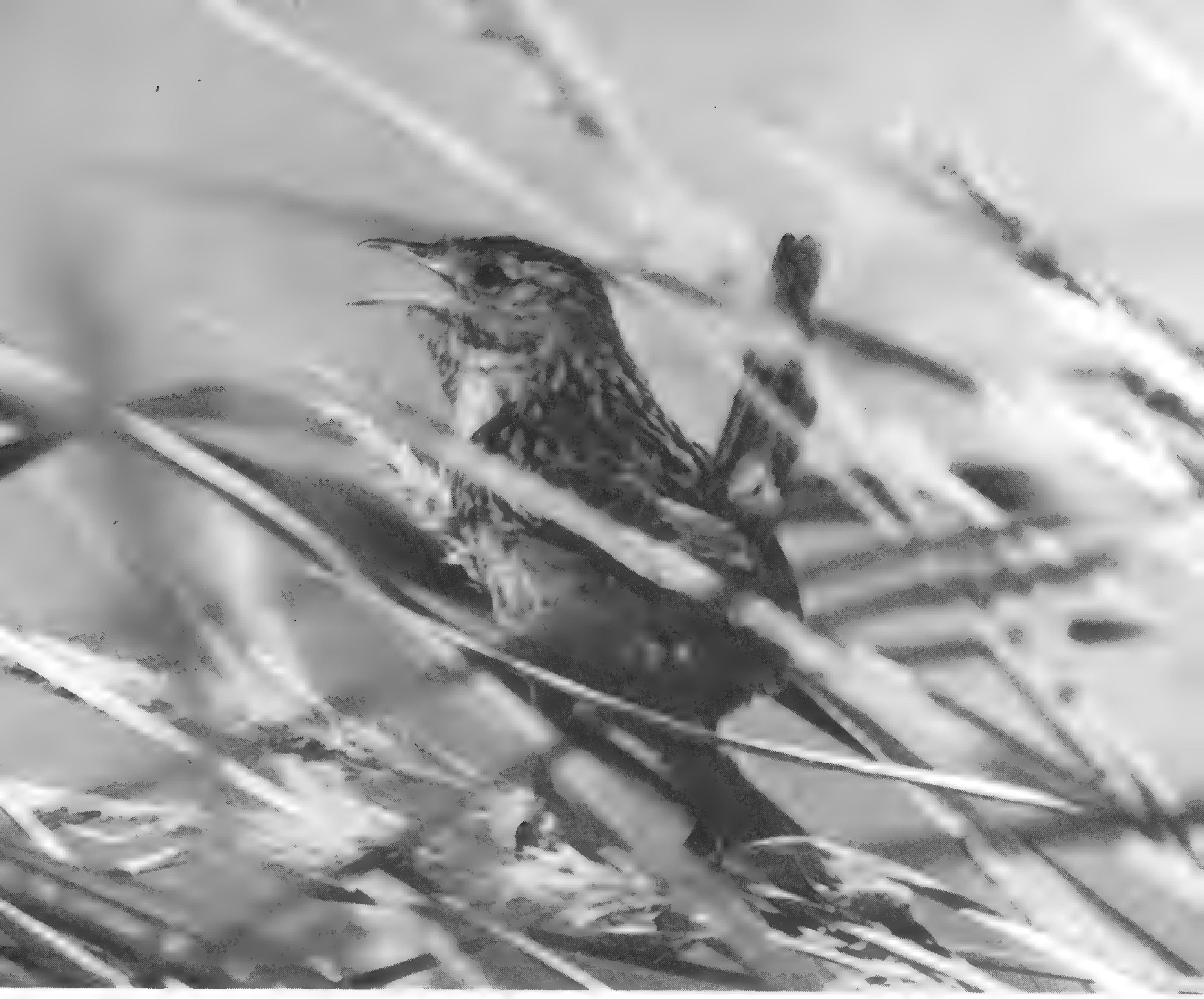


Figure 11. A Grass Wren singing from atop a tussock clump on Kidney Island during a brief windless period. When the wind is strong — very often — the wren sings from beneath a canopy of tussock grass.

1962 and his latest was an adult feeding juveniles on 4 December 1960. The nest that he found on 9 October was at Moody Valley, about a foot above ground in a clump of rushes and overhung by rush blades and some grass. The nest itself was a rough ball of grasses well lined with white feathers, probably a gull's. When he revisited the nest on 7 November, two of the young fledged, each going a different way.

Grass Wrens tend to be not only quite sedentary in the Falklands but also closely attached to a specific area, probably the year round. Near the hut at Kidney Island, one wren trapped and banded 4 January 1959 was retrapped the following 19 November, and another similarly caught and marked 26 October 1962 was retrapped exactly one year later, both close to the hut (Woods, pers. commun.).

*Remarks.* — In Tierra del Fuego, the Grass Wren is a breeding resident, found in marshes and grassy areas (Humphrey *et al.*, 1970). Crawshay (1907:44) was impressed by its ability to subsist in winter. In Argentina, Wetmore (1926:349–350) came upon "a small colony" at Lavalle "in low growths of dead rushes at the border of a tidal marsh" and encountered other individuals near Tunuyan "in growths of heavy weeds along irrigation ditches, in small marshes, or in corn fields." At Lavalle, his attention was attracted to the birds by their "tinkling songs *tu-tu-tu tee-tee-tee ter-ter-ter tsee-ee-ee-ee*, each triplet being pitched in a slightly different key, while the whole terminated in a metallic music-box rattle." When he succeeded in flushing them from the rushes, he noted that their flight was undulating.

## HOUSE WREN

(Figure 12)

*Status.* — Common resident on certain tussock islands where it frequents the adjacent beaches, rocky slopes, and cliffs. Nesting season: October through December.

*Observations.* — Despite their small size, House Wrens were remarkably conspicuous elements in the abundant avifauna of Kidney Island — the only place where we encountered them. From our first day, 3 November 1953, they impressed us by their abundance, animation, and tameness. They were everywhere among the boulders and loose rocks on the beach and in the adjacent tussock grass. They fluttered from one rock to another, disappearing below and scurrying along mouse-like under them, popping into view a few feet distant and then vanishing again. They made hasty trips to the rows of washed-up seaweed and kelp where, with the dexterity of Austral Thrushes and Tussockbirds, they flipped over pieces of debris in search of food. From the beach they fluttered back into the thick foliage of the tussock grass, soon reappearing. All the time they were indifferent to us, although always managing to stay out from under our footsteps.

There was much singing. Some males discharged their volleys while perched on the higher rocks, others on the stronger tussock blades. A few even sang under the ledges and loose boulders along the beach. The songs, only mildly suggestive of those of the North American population, consisted of a loud, explosive series of trills and warbles, usually of short duration. Their alarm notes, one or more *churrrs*, were like those of the North American population.

I found one nest with four well-developed young on 4 November. This was in one of the taller tussock clumps that fringed the beach. The adults going into the clump with food in their mouths gave the site away; but it was only after I had poked deeply in the grass that I at last discovered the entrance leading into a ball of dead grasses, lodged in a hollow among the roots on the side of the pedestal, three feet above the ground. Both adults alternated in bringing food, usually gathered on the beach. The young were still in the nest on 5 November, but were out of it, though close by, the next day. As I approached the site, both adults *churred* repeatedly. When I eventually disturbed a fledgling that had been sitting motionless, instantly one of the parents went into an injury-feigning display, fluttering its wings, spreading and lowering its tail, and dropping from one grass blade down to another while working its way deeper into the tussock grass.

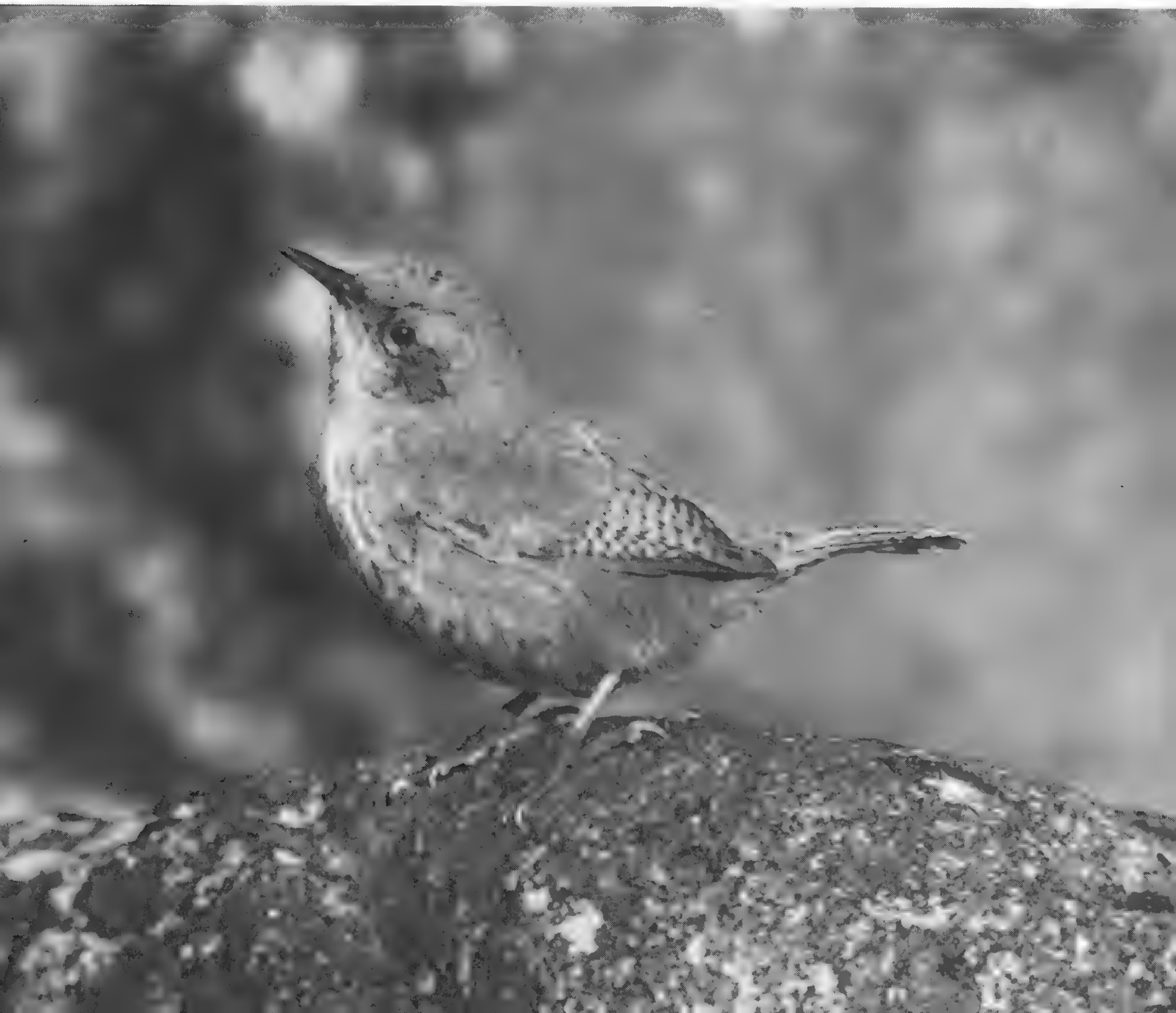
Robin Woods (pers. commun.) found two nests on Kidney Island in the sides of tussock pedestals. One, 2.8 feet above ground with entrance at the end of a one-foot tunnel, was constructed of grass stems and lined with large dark brown feathers of the Turkey Vulture (*Cathartes aura*). When discovered on 20 November 1961, it contained three nestlings with eyes still unopened. The other nest, 2.0 feet above ground, was just inside the pedestal without a tunnel leading to it. On 30 October 1963, it contained four nestlings a few days old. When Woods (1970:20) later dismantled the nest, he noted that it was built mainly of grass stems intermixed with tussock root fibers, hairs of the sea lion (*Otaria byronia*), and feathers. Much of the lining was of root fibers, but feathers — 255 from at least seven bird species — almost equalled them in bulk.

Besides nesting in tussock clumps at Kidney Island, House Wrens may choose other sites. Woods (1970:19–20) stated that they can be in "crannies between large rounded boulders at the top of the beach." J. E. Hamilton (*in* Cawkell and Hamilton, 1961:23) spoke of the House Wren as nesting "under a rock."

I was soon convinced, after a few days on Kidney Island, that the principal habitat of the House Wren comprised the outer edges of the tussock cover and the adjacent beach and cliffs. This was in marked contrast to the Grass Wren's habitat, described in the preceding account, which was the tussock cover of the interior. At no time did we see the House Wrens far from the beach and cliffs.

Between 28 November and 5 December, the House Wrens were more numerous, due to the addition of many young-of-the-year. Although full

Figure 12. A House Wren on the boulder-strewn beach at Kidney Island. The beach above the high-tide line supplies much of its food; the bordering clumps of tussock grass provide sites for nesting.



grown, they were nonetheless readily recognizable by their darker, more richly brown plumage, whereas that of the adults was distinctly grayish from wear and fading. They were also noticeably tamer. When they emerged from the rocks at my feet, they showed total unconcern. If they flew away from me, it was only to avoid being stepped on. One youngster inadvertently hopped onto the toe of my boot where it rested for a few moments, in no hurry to move on.

The young by this time were independent of their parents, although occasionally we saw individuals approach an adult to flutter their wings and gape hopefully without success. Now and then a youngster attempted a song, but it amounted to no more than a few wheezy trills. I noted one youngster try to copulate with another, only to be repulsed quickly.

We heard very little singing by adults during this period and saw no evidence that any adults had nests. The breeding season seemed to be almost over.

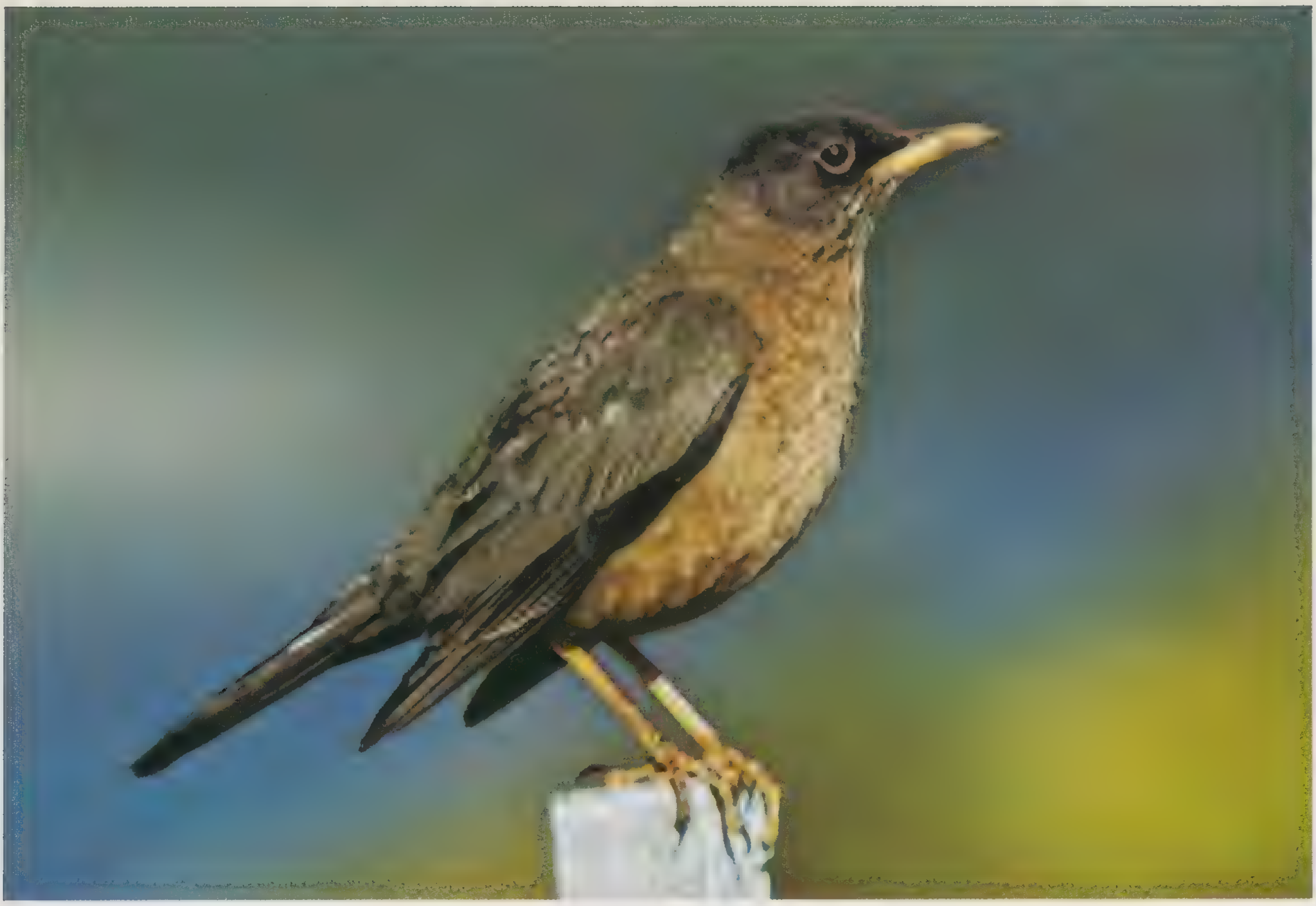
Between 12 and 27 February, we noticed no reduction in the size of the population. If anything, it seemed even larger and more animated. There was no distinguishing the young from most adults now as the adults had just about completed their molt into a darker plumage.

We observed many wrens scurrying over the steep cliffs and ledges in the penguin-cormorant colony where we had seen only an occasional individual before. They were foraging for insects and other food in and between vacant nests. Along the rocky beach we noticed almost constant activity. Not only was there the usual amount of flying about and foraging, but also considerable quarreling on the rocky part of the beach as if territories were being disputed. Time and again I watched one individual challenge another by arching and waving its wings over its back, lowering its tail, opening its mouth, and darting toward another, which more often than not retreated. Any squeaking by me almost invariably started all the wrens within hearing distance, in the tussock grass or among the rocks, into a frenzy of *churring* and hopping with tails lifted vertically. At no time did I note a song or an attempt at one. As the wrens were rather evenly distributed, I suspected they were maintaining territories. Whether such areas were their breeding territories being held now for feeding and roosting through the winter, I had no way of knowing.

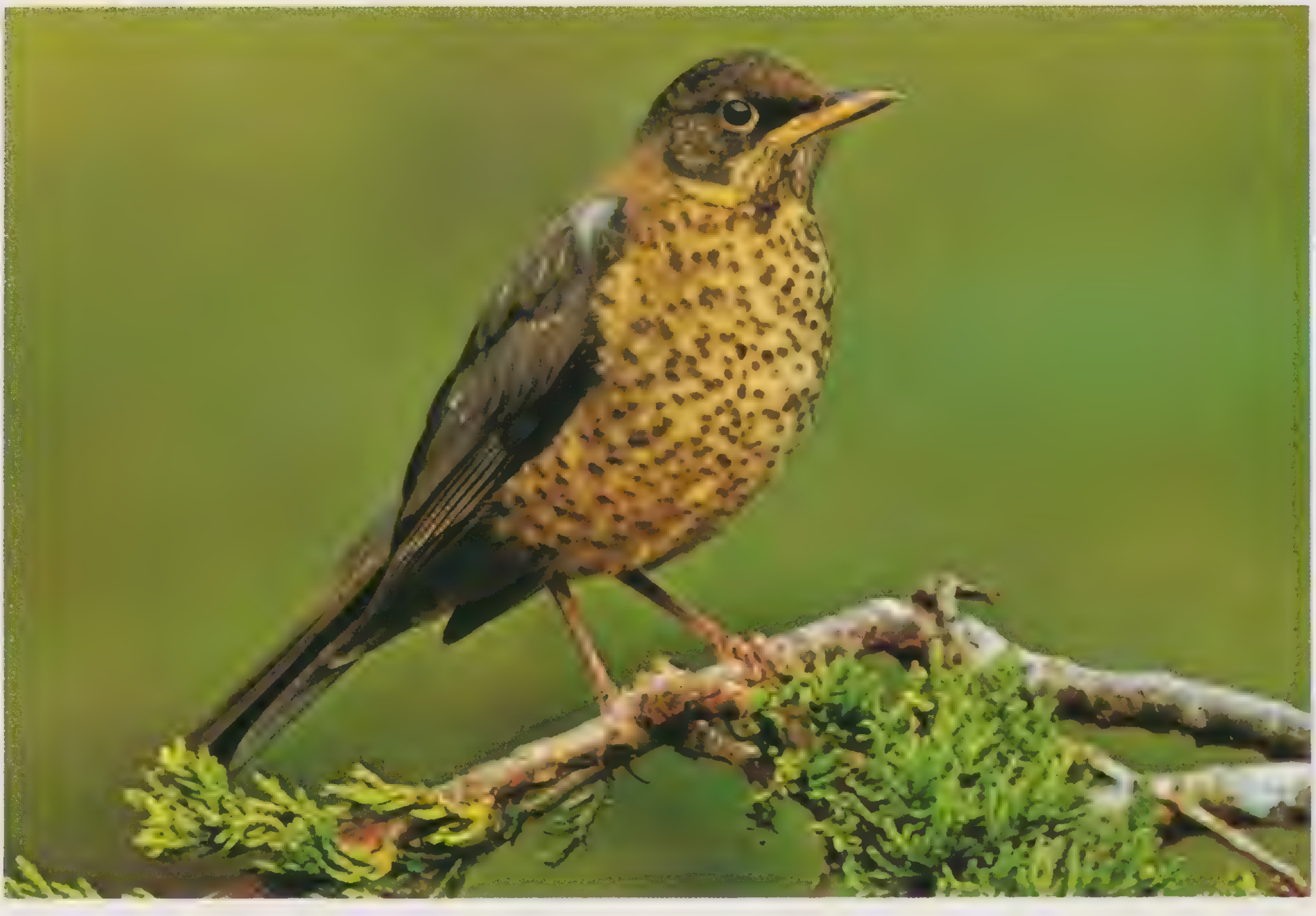
On the evening of 19 February, long after dark, a House Wren flew up from my feet into the beam of my flashlight as I was walking over the rocky beach. This was proof that at least some of the wrens sought shelter during the night under the rocks rather than in the tussock grass.

Although we did not find any nests of the House Wren on Kidney Island in 1971–1972, our observations of their abundance and behavior substantiated those made 18 years earlier.

The restricted distribution of the House Wren in the Falklands was puzzling. The species appeared to require the seaside fringe of an extensive and luxuriant growth of tussock grass on small islands. We never saw it in any other kind of habitat. Yet the existence of a habitat that appeared, outwardly at least, to meet the species' requirements was no assurance that the species was present. For example, Coffin Island, near New Island, had a large population of the House Wren, while Fanning Island in San Carlos waters had no House Wrens — determined by us after a thorough search. Both islands were ideally tussock-covered and had suitably rocky shores.



*Above,* Austral Thrush, *Turdus falcklandii,* adult.
*Below,* Austral Thrush, *Turdus falcklandii, immature.*



Evidently there was some critical factor, such as available food supply or the extent of predation, or a combination of factors, that limited the distribution of this species.

*Remarks.* — In southern South America south into Tierra del Fuego, the House Wren is apparently a familiar breeding species. It is quite plentiful in the Andes up to about 8,000 feet (Johnson, 1967:301) and, at least in Tierra del Fuego, it is migratory (Humphrey *et al.*, 1970:292–293). Descriptions of habitats and nest sites given by Johnson (1967:302) and Wetmore (1926:347–348) and other descriptions assembled by Humphrey *et al.* (1970:292–294) could easily apply to the North American population of the species, since it frequents brushy areas and woodland edges, appears about ranch buildings, and nests in a variety of cavities including fence posts and nest boxes. The Falkland population, by contrast, is remarkable in its sharp, year-round restriction to a few tussock islands. To my knowledge, there is no record of a House Wren seen in Stanley or in the outlying farm settlements, despite the prevalence of tree and shrub plantations, many hedgerows, and numerous cavities in sheds and dilapidated buildings.

## AUSTRAL THRUSH

(Plate II)

*Status.* — Common and widespread resident in nearly all places where rocky outcrops, ravines, shrubbery, or anything else provide shelter. Particularly numerous on tussock islands and their beaches and about settlements with tree and shrub plantations. Nesting season: September through January.

*Observations.* — This species, in its general form, habits, and behavior, was as much a robin as the well-known North American bird, *Turdus migratorius.* And it was no less tolerant of a wide variety of habitats. Only in its darker and drabber feather coat, bright orange-yellow bill and feet, and less melodious vocalizations was it notably different.

Our acquaintance with the Austral Thrush began on 24 October 1953 at Charles Point where there was a military installation — lookout hut, storehouse, gun emplacements, and assorted sheds — open, ramshackle, and abandoned since World War II. A family of thrushes were the sole residents, and this day both were feeding one stub-tailed fledgling — their only offspring — recently out of the nest. During the time we were there, until 1 November, the youngster stayed close to the buildings, always on the lee side when the winds blew strongly. All day on 31 October, while a gale raged, the young bird remained in one place out of the wind. It called frequently and was fed with remarkable regularity by the female, which managed to find food somewhere and combat the face of the wind each time she returned.

We found old thrush nests, some quite recent, in all the buildings and several more in crevices of the sea cliffs below the installation. There was no question but that this spot had been favored by thrushes, probably no more than a pair at a time, ever since its abandonment.

Thrushes were quite numerous on Kidney Island when we arrived on 3 November. They sang from high clumps of tussock grass, the crests of boulders on the beach, the edges of ledge shelves — any place that offered

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Plate II. Austral Thrush, *Turdus falcklandii,* adult (*above*) and immature (*below*).

a conspicuous perch. One male's territory was the vicinity of our hut where he sang from the roof, also the nearby shed and several posts. He accepted bread crumbs that we put on a board outside the hut door; if we left the door open, he hopped into the hut, looking for additional sustenance on the floor. But this bird apparently did not have a mate and we found no evidence of nesting by any of the thrushes on the island at this time.

The thrush's territorial song consisted of whistles with *tee-you, churr,* and *tee* notes, given in varying number and order. For example: *wee, wee, tee-you, tee-you, churr, tee;* or *wee, wee, churr, tee, tee-you.* At dawn the song was continuous for many minutes. The whole song was usually muted and not audible at any great distance. The only calls we heard commonly were a loud, harsh *kreeep* given in rapid succession, as when alarmed, and a loud sighing sound, *wheee,* of undetermined function, often repeated while the bird was quietly perched.

The thrushes seemed well adjusted to the peculiarities of Kidney Island. They moved under and around the tussock clumps, seeking food in the soft, moist soil that was often matted with liverworts and other tiny herbaceous plants. Frequently they pecked vigorously at the ground to uncover grubs or, in many cases, camel-crickets. They seemed to spend more time, however, foraging in the plant debris washed up on the beach, often ignoring us standing only a few feet away. Like the Tussockbirds, in whose company they commonly appeared, they were adept in flipping over pieces of dead kelp or pecking holes into the dense rows of rotting kelp and seaweed where they uncovered quantities of amphipods. Frequently they drove Tussockbirds from holes they had started, and dug deeper.

On 13 November, in Government Forest in Stanley, we saw two nests in macrocarpa, in each case about five feet from the ground. One contained a nestling about five days old, the other three blue eggs speckled brown, more heavily toward the larger ends. Our intermittent observations on these two nests in the next 13 days revealed that both sexes participated in feeding the nestling in the first nest, but only the female incubated eggs in the second. The adults were only moderately wary of us, returning to their nests while we stood as close as 15 feet. The incubating female sat closely. On leaving, when we were almost touching the nesting tree, she merely flew to a nearby perch, protesting with loud *kreeep* notes. The eggs hatched on 26 November. During this day, when the sky suddenly cleared and it was almost instantly warm in the shelter of Government Forest, I saw the female leave her nest and fly down to an open grassy spot where she lay on her side in the full sunlight, fluffed out her body feathers, stretched the upper wing fully, closed her eyes, and remained motionless for about four minutes — obviously reaping physical enjoyment in this respite from the cloudiness and chill.

When we returned to Kidney Island on 28 November, we found the male near our hut with a mate and discovered their nest on 1 December, four feet up on the side of a tussock clump, constructed entirely of grass, and overhung and almost completely concealed by tussock blades. There were two nestlings in it.

In mid-November 1971, we found thrushes as numerous on Kidney Island as they had been 18 years earlier. We watched one pair repeatedly carrying food to young in a nest not far from our hut but we failed to find the nest itself. On 26 November in Stanley, Maurice Rumboll found a nest, 10 feet up in the crotch of a macrocarpa, with two nestlings three to four days old. At Port San Carlos and West Point Island in early December, we saw fully grown juveniles in spotted plumage. Our search for nests yielded only old ones — three in woolsheds and one under a jetty at Port San Carlos and two in macrocarpas six and eight feet from the ground on West Point Island.

All the nests that we examined in the Falklands in 1953 and 1971 were bulky — the one on Kidney Island in 1953 had an over-all diameter of 12 inches. Coarse grasses were used for the walls and finer grasses for the lining. Only one nest — an old one at Stanley — that I pulled apart contained mud which was in the bottom and formed part of the lower wall. Robin Woods (pers. commun.) noted that all the nests he found on Kidney Island were made completely of grasses but that most of the nests he found in Stanley and elsewhere contained mud or dung.

The nesting season seemed to be over by January. Although we noted thrushes very commonly about the settlement at New Island in late December of 1953 and 1971, there was no singing and there were no stub-tailed juveniles observed thereafter. The thrush population about the settlement remained impressive in its numbers and activities. Half the population consisted of young birds still in juvenal plumage or, toward the end of January, in various stages of the postjuvenal molt. The adults were molting heavily throughout January.

In Stanley and about settlements, the thrushes foraged for earthworms and insects, including caterpillars, on lawns and hard-grazed sheep paddocks. For earthworms they practiced the same hunting techniques as American Robins — hopping a short distance, stopping abruptly to cock their heads at burrows, and driving their bills into them if they seemed productive. For insects they entered sheds on occasion, and for both earthworms and insects, including beetle grubs, they frequented gardens. When a person dug potatoes, a few thrushes were often on hand, fearlessly searching and poking into the soil as soon as it was upturned. And much to the annoyance of gardeners who had just planted seeds, they opened up the furrows in their avid searches, exposing the seeds but not eating them. Now and then thrushes varied their diet by eating the berries of diddle-dee. At New Island in January we saw thrushes, sometimes several at a time, flying from the settlement to the adjacent high slopes where diddle-dee abounded for a quick feast on the fruit, then swooping and sailing back into the settlement.

In February 1972, inland from Volunteer Beach, we saw thrushes in flocks, ranging in size from 15 to 50 individuals, feeding on the berries of diddle-dee that were thriving in extensive patches. During the same month at Kidney Island we noted fewer thrushes on the beach even though Tussockbirds and House Wrens were as abundant as they had been earlier. We surmised that this reduction in number was due to the departure of most individuals to places where diddle-dee berries offered more enticing food.

*Remarks.* — In Tierra del Fuego, the Austral Thrush is a common breeding resident with a strong preference for brushy country and the vicinity of forests at most any elevation (summarized from references quoted by Humphrey *et al.*, 1970:295–297). This being the case, it is understandable why the Austral Thrush in the Falklands should find the vicinity of settlements with their shrub and tree plantations innately attractive, even though it had first established itself in tussock islands and other sheltered places.

The nesting season of the Austral Thrush is notably prolonged, owing apparently to its being multiple brooded. Cawkell and Hamilton (1961:24) stated that it rears two and even three broods; they also reported a pair that raised three broods after the initial clutch was taken. Woods (pers. commun.) is convinced that the species regularly rears three broods in a season. He found a nest with eggs as early as 8 September 1957 and a nest with large young as late as 28 January 1959 — a time span of nearly five months. From his study of five nestings in Stanley, he determined that the incubation period was 14 to 16 days from the last egg laid, the broods required from 16 to 18 days before fledging, and the interval between one nesting and the next was 12 to 14 days. Thus, between early September and late January, there was ample time for one pair to rear three broods.

## CORRENDERA PIPIT

(Plate III)

*Status.* — Common resident in exposed inland areas or heaths where white grass predominates. Much less common in areas where diddle-dee is extensive. Nesting season: late September through early January.

*Observations.* — During our second prolonged stay in the Falklands, from November 1971 to the following March, we saw much of the interior by Land-Rover. As we traveled over grass-covered heath, Correndera Pipits occasionally jumped up just ahead of us, flashing the white outer tail feathers as they mounted jerkily upward with several fast wing-strokes, then a slight dip down, then up a little higher each time, and so on, until they dropped down at a safe distance.

In 1953, we found the pipits already flight-singing by 24 October above the grassy slopes of Sappers Hill south of Stanley. There were as many as a dozen males performing here on 13 and 14 November. Each performer mounted into the air to a height of 50 to 75 feet, in a few cases higher, climbing rather abruptly into the wind with body at a slightly vertical angle, if the wind was moderate, or at a sharper angle, if the wind was strong. At about 25 feet from the ground he began singing; at the zenith he continued singing, facing the wind and fluttering his wings, neither moving forward nor changing elevation. When the wind was particularly strong, he was often carried backward while still facing into it. In descent he set his wings and either spiraled downward, tipping his body from side to side as he banked with each turn, or simply volplaned downward into the wind. The duration of each performance by one individual — from the moment he left the ground until he returned — varied from one to 10 minutes with about four minutes being the average. The full song at the zenith was *per-teetle-tee, per clee tee; per-teetle-tee, per clee tee,* etc., repeated steadily. During descent the performer ceased the full song, and began uttering an irregular series of *zeee-ee* calls, occasionally with a *per-clee-tee* interspersed.

On several occasions, a male terminated his descent by pursuing another pipit, probably a female. Only once did I see what was obviously a territorial dispute between males. They clashed in midair, face to face, each one striking the other with beak and claw. Once I saw a male with food in his mouth suddenly approached by another adult, presumably a female, which took the food and then was closely chased by the male for a considerable distance.

On 24 November, I found one nest with four eggs, sheltered by a few overhanging blades of white grass. The nest itself was a simple cup made of grasses. My discovery was aided by the behavior of the female which, at my appearance in the immediate vicinity, took to the air and circled above me, uttering repeatedly *click-click-te, click-click-te,* in protest. Assuming that I was too near the nest, I walked away until I was far enough to allay her disturbance, then watched and waited. In due course she went down to what proved to be the nest site. When I approached to within two feet of the nest, she sneaked off with a "rodent-run," tail spread and depressed, wings extended and flopping on the ground. The whole act was a perfect distraction display — surprising in the Falklands where there are no native land mammals or other ground molesters that might induce such an act. I could only surmise that it was a response inherited from those forebears of the species in continental South America where there are ground predators.

The female was the only bird present when I found the nest or, on later occasions, when I visited it. Normally, after flushing her — she did not give the distraction display again — she stayed more often in the air above me, circling and protesting vocally, than standing on neighboring rocks or walking around me. The eggs hatched about 28 November and the young fledged from the nest about 10 December, 12 days later. On 11 December, when I last visited the hill-top, there were several adults protesting my presence — an indication that more young than those in the nest I had found were out of their nests.

At West Point Island on 16 December 1971, we discovered a nest with four eggs in thick, 12-inch-high grasses that bent over and completely obscured it. The eggs hatched two days later. (Years ago Brooks, 1917:159, reported a nest on the same day in December "with two eggs and two young about to hatch.") On the several occasions when we later visited the nest, the attending bird flushed and disappeared out of sight without the slightest protest and not even a suggestion of a distraction display.

As far as we could determine, Correndera Pipits are entirely insectivorous. Cawkell and Hamilton (1961:24) reported them catching "blowflies." Robin Woods (pers. commun.) watched adult birds on two different occasions catching moths.

What becomes of Correndera Pipits after the nesting season? Cawkell and Hamilton (1961:24) stated that they are "certainly less numerous," implying that at least some of them leave the Falklands. Woods (pers. commun.) observed seven instances of movements over the coast in March and April that strongly suggested migratory activity. Yet Stuart Booth (pers. commun.) observed pipits remaining in or near their territories throughout the year. In the winter of 1972 he saw them singly, sometimes in pairs, and occasionally in threes.

*Remarks.* — The breeding season of the Correndera Pipit is remarkably long. Booth (pers. commun.) noted pipits flight-singing 20 and 27

August in 1972. Woods (pers. commun.) recorded flight-singing as early as 11 August in 1962 and as late as 25 January in 1959, 5 March in 1962, and 9 April in 1961. His earliest dates for nests were 19 October 1957, a nest with four young which fledged 31 October, and 21 October 1957, a nest with four eggs; his latest dates were 25 December 1957 (a nest with two eggs, which hatched 8 January 1958) and 26 December 1959 (a nest with two eggs). The nesting season in the Falklands evidently coincides with the nesting season for Correndera Pipits in Tierra del Fuego where they are breeding summer visitors, a few overwintering (Humphrey *et al.*, 1970: 299). Thus, Crawshay (1907:47) saw about 30 occupied nests, one as early as 16 October and others as late as "about the beginning of January."

The strength of most winds seems not to deter Correndera Pipits from flight-singing. Cawkell and Hamilton (1961:24) reported three birds singing aloft in a wind blowing at about 30 knots (=35 miles per hour), nearly gale force. It is doubtful, however, that pipits can successfully flight-sing in winds blowing much faster.

## LONG-TAILED MEADOWLARK

(Plate I)

*Status.* — Widely distributed in inland areas or heaths with grassy cover often intermixed with diddle-dee and/or other dwarf shrubs. Common near settlements with shrub and tree plantations and in sheltered ravines with suitable grassy cover and shrubby vegetation. Nesting season: August through December.

*Observations.* — The form and general behavior of this large red-breasted meadowlark reminded us at once of the North American yellow-breasted meadowlarks with which Short (1968) recently considered them congeneric. Generally wary and rangy — with exceptions to be mentioned later — it took flight at the slightest alarm and moved a great distance away from us. It flew steadily and strongly but without the intermittent intervals of sailing characteristic of North American meadowlarks. On alighting, frequently on a shrub, rock, or mound, it stood upright and alert. Its principal calls, given either in flight or when perched, were an abrupt *kimp* and a louder *kreeko*, often uttered when alarmed.

At York Bay on 26 October 1953, we watched a pair among the sand dunes, walking about in a busy search for insect food. From time to time the male, whose crimson breast was almost startling when he faced us, flew to the top of the highest dune and sang a short, unmusical series of rusty, somewhat abrasive notes: *skree, skree, skreeel, screech, screech.* The singing was soon over as he returned to the ground to join his mate. This performance — flying to the highest available point and singing for a short period — was typical of most males that we observed later, with the exception of a few times when we noticed them singing in flight as they moved from one point to another.

At New Island in 1954, Tony Felton gave me two eggs from a clutch of three that he took from a nest in late October. The nest itself was bulkily constructed of grasses, open at the top — not domed or semidomed — and situated in the crown of a tussock clump, well sheltered by overarching tussock blades. The eggs, large and conspicuous, were white, faintly

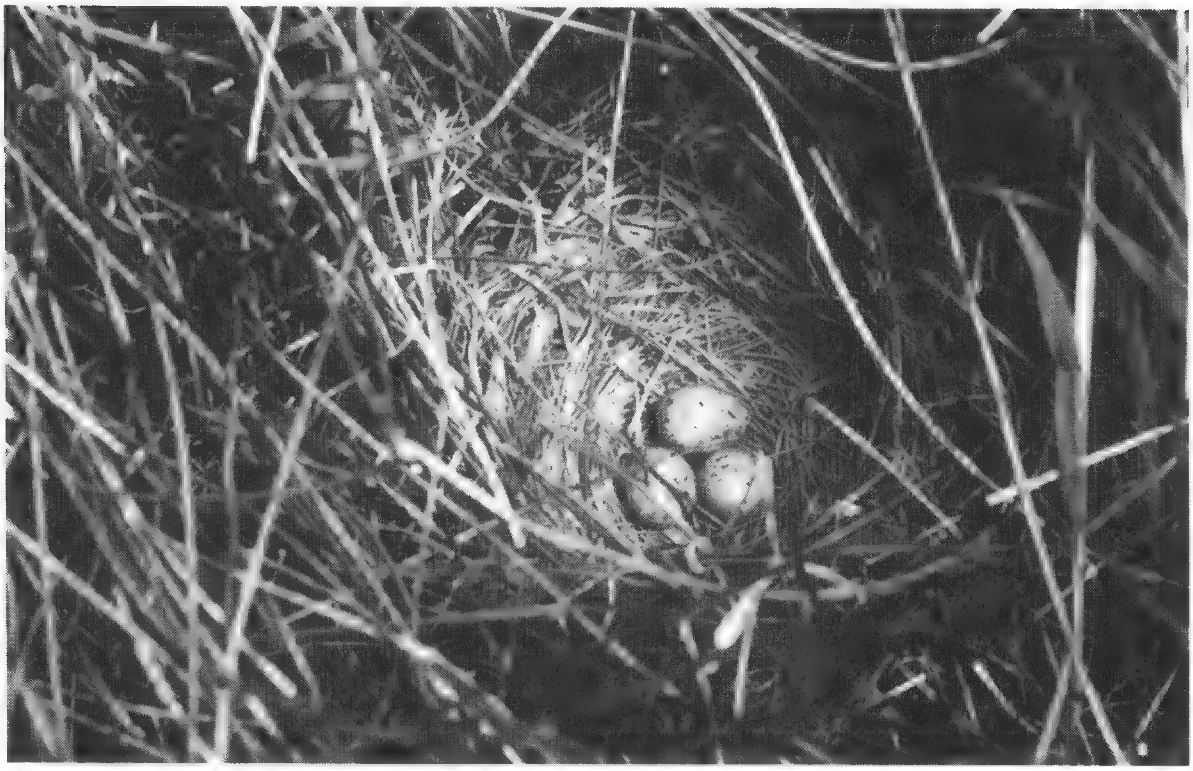

Figure 13. Nest of a Long-tailed Meadowlark, West Point Island, without doming. This was the case with all the nests we found.

marked all over with tiny speckles and violet splotches together with scattered blackish spots and scrawls.

At West Point Island, 13 December 1971, Timmy May showed us a nest on the ground in the middle of a 15-inch-high clump of gorse about 10 feet in diameter. Constructed of grasses and open at the top, the nest contained three nestlings about six days old and an egg. The basic color of the egg was off-white, speckled brown all over with a few blackish scrawls. Later, on 20 December, Bruce May showed us a nest (Figure 13) on the ground, sheltered partly by surrounding 12-inch-high rushes. Also open at the top, the nest contained three eggs that were similar in color to those described above except that they were without scrawls. The females attending both nests flushed from them and disappeared, showing no concern. Bruce May showed us another nest, empty, that was only 60 feet away in the rushes. It had been occupied in October —in all probability by the same pair.

Robin Woods (pers. commun.) found two nests on the outskirts of Stanley. One, discovered on 30 September 1958, was in white grass and had a curved, three-foot-long pathway of flattened grass leading to it. In the nest were three eggs which hatched on 4 October. The other nest, discovered on 19 September 1957 while being built, was in long white grass. Three eggs appeared in the nest on consecutive days, 23, 24, and 25 September. Both nests were simple cups made of grasses.

Between the dates when we were shown the nests at West Point Island, we noted from day to day around the settlement a family with three fully grown, flying young being diligently fed by both parents. While the young waited in the shrubbery, both parents sought caterpillars and grubs in the nearby sheep paddock. To secure grubs they probed deeply, using their bills which were exceedingly long for an icterid and very sharply pointed

— much more so than those of North American *Sturnella.* On securing a grub, the parent flew with it to an offspring which, after begging with open gape and fluttering wings, took it hungrily.

The meadowlarks at West Point Island were notably tame about the settlement, where they sang from fences, ridgepoles of buildings — almost anything elevated. This was the case, too, at New Island in 1953–1954 and 1971–1972. Here, during both stays, we watched families with dependent young in January. Many times the parents sought insect food for their young from under dried cow chips near the settlement. With remarkable skill each bird first inserted the bill beneath a chip and then flipped it over quickly, picking up the exposed insects before they could escape. When its mouth was full, the bird flew to one of the begging youngsters and poked the contents into the wide open mouth.

The meadowlark has a long breeding season. Cawkell and Hamilton (1961:25) stated that the meadowlark may be heard singing in the period of May to August and that nests can be found "as early as the end of August." Their statement is corroborated by Woods (pers. commun.) who found a nest half built on 25 August 1958. This further suggests the strong possibility that the meadowlark may regularly have two broods each breeding season.

Primarily insect-eaters, meadowlarks served all agricultural interests in the Falklands very well. Gardeners, nonetheless, complained bitterly about one vagrancy in the diet — a predilection for new potatoes. On discovering potatoes uncovered by wind erosion or left on the ground after being dug, meadowlarks readily punctured holes in them and savored the contents.

By February, we saw meadowlarks in small flocks, which flew from place to place in loose formation, all the while giving the loud *kimp* call. They then alighted on the ground, walked or ran about in quest of food, and were off again. Cawkell and Hamilton (1961:25) reported flocks in winter with as many as 60 individuals.

*Remarks.* — Although Short (1968:24) generalized from several sources — for example, Johnson (1967:337) — that all the species of meadowlarks which he has grouped in the genus *Sturnella* "build a ground nest that is characteristically domed or semidomed, with a side entrance," the nests we saw in the Falklands were open at the top with no doming whatever. Sources quoted by Humphrey *et al.* (1970:306) on nests of the Long-tailed Meadowlark in Tierra del Fuego do not mention doming as a structural peculiarity. Doming may not be typical, therefore, of the species as a whole.

## BLACK-THROATED FINCH

(Plate III)

*Status.* — Common resident inland; nesting on the heath where white grass is interrupted by frequent patches of diddle-dee; foraging on lawns about settlements or on valley or coastal greens where there is hard grazing. Nesting season: September through early January.

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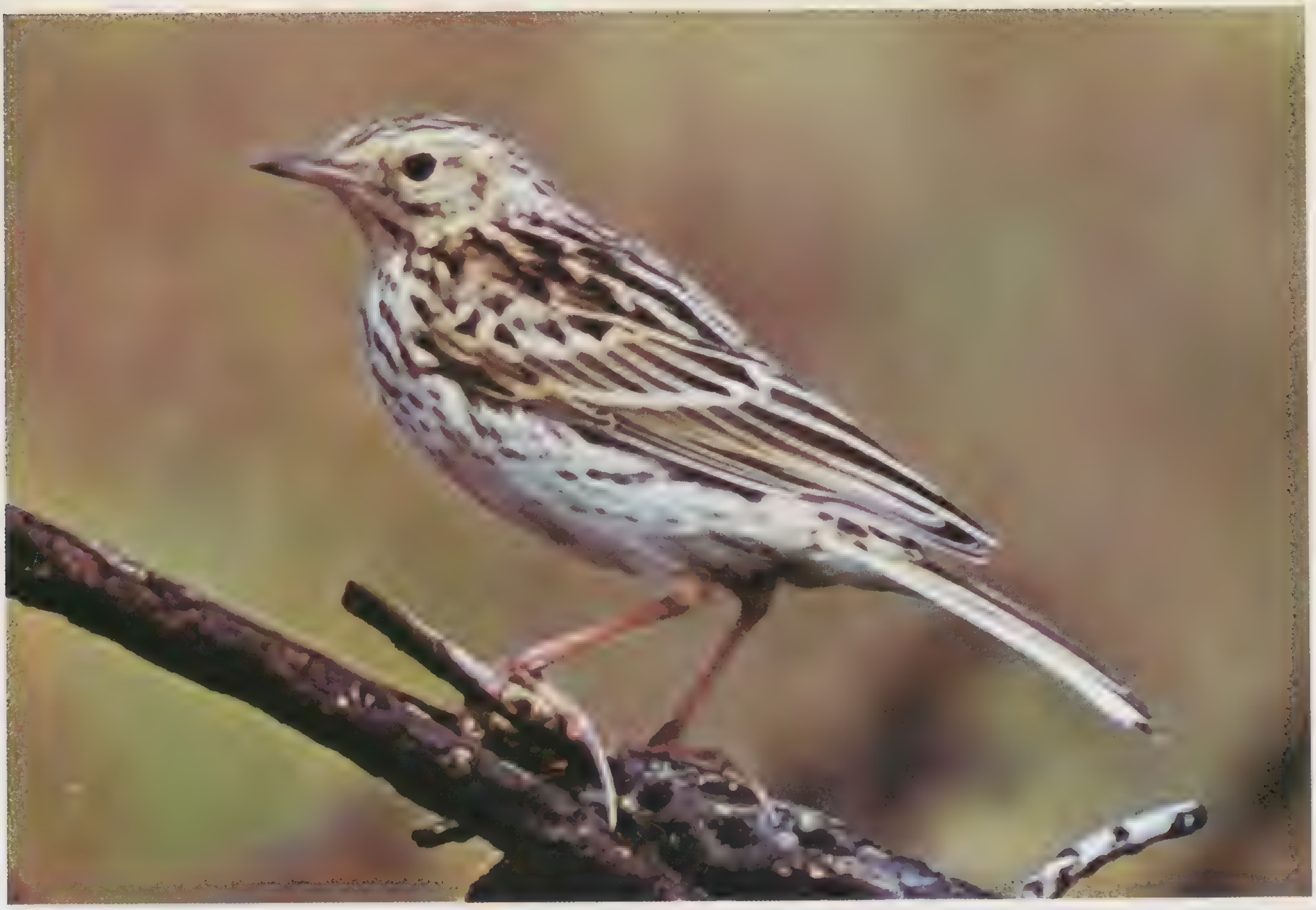
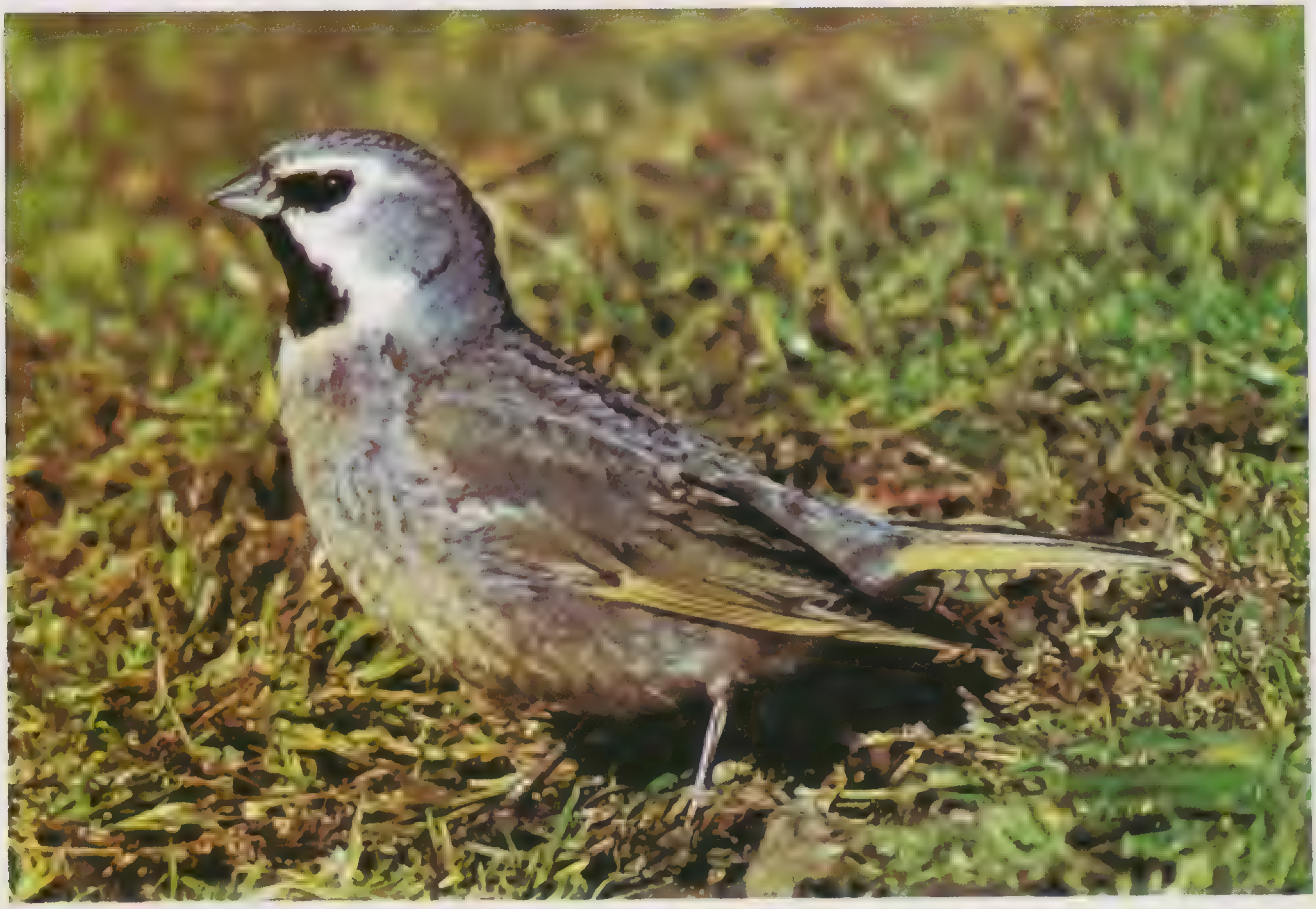
Plate III. *Above,* Correndera Pipit, *Anthus correndera.*
*Below,* Black-throated Finch, *Melanodera melanodera.*



*Above,* Correndera Pipit, *Anthus correndera.*
*Below,* Black-throated Finch, *Melanodera melanodera.*



*Observations.* — In the period between 24 and 28 October 1953, we saw Black-throated Finches in flocks of a dozen or more on the outskirts of Stanley, passing in undulating flight or stopping to feed on the closely cropped lawns in front of Government House. The males sang sporadically and now and then chased one another, but we saw no isolated pairs. This was evidently an oversight, because nesting was already underway — a fact corroborated later when, on 27 November, Edwin Cawkell told me about a nest found that day with three well-developed young. Not until 31 October at Charles Point did we begin seeing isolated pairs. Nevertheless, throughout the rest of the nesting season, we still continued to see small flocks feeding or visiting shallow pools to drink and bathe. Apparently this species was territorial to the extent that pairs established and defended small areas for breeding and nesting purposes only. When leaving their territories to feed or bathe, they were tolerant of their fellows and often joined them.

The one nest we found, at Arrow Point on 9 December, contained four eggs and was sunken deep in a hummock completely surrounded by water. A few sprigs of diddle-dee and blades of white grass reached to the edge of the nest but did not cover it. The nest was comprised of grasses and thickly lined with wool. Stuart Booth (pers. commun.) found a nest with three eggs, 12 November 1972, that was similarly lined with wool. We discovered the Arrow Point nest by following the female to it. She showed no concern when we flushed her — she simply dropped down nearby and watched us. We did not see the male.

Robin Woods (pers. commun.) obtained records of nine nests. The earliest, found 26 September 1958, contained three eggs; the young left it on 17 October. The latest, found 28 December 1957, contained three eggs that hatched on 4 January 1958; the young left it on 21 January. The nests were variously lined, some with soft feathers and one with many feathers and horsehair.

The male's territorial song, given in sunny, calm weather from a rock or any other promontory available, was a short, subdued, though nonetheless pleasing, series of whistles and warbles, one whistle usually alternating with two lower notes — *weee, tu-lu, weee, tu-lu,* etc. — many times repeated. We rarely noted a bird singing in a high wind; when we did, it was barely audible. A variation of the territorial song was sometimes *weee, tu, weee, weee, tu,* etc. During flight, either sex uttered a clear *weee-o-weee,* somewhat reminiscent of the call of the Black-bellied Plover (*Squatarola squatarola*), though not as loud. Another note was a *peet, peet-let,* like a pipit's, given when an individual was suddenly flushed or otherwise alarmed. Still other notes were faint, barely audible *eeep* or *teep* sounds produced repeatedly by all individuals when they were together in flocks, flying or feeding.

Black-throated Finches are assiduous seed-eaters. Small flocks frequented a weedy area fringing a dump near Stanley. Here we watched them obtaining seeds of dandelions (*Taraxacum* sp.), 24 November 1953. Each bird pulled down a fully mature head, then picked out the seeds one by one, shaking off the attached down before cracking the seeds and swallowing them. At settlements that we visited in the Falklands in 1971–1972, we saw small numbers, sometimes close to buildings, foraging industriously, almost machine-like, on tiny seeds fallen from the lawn grass or seeds from the heads of English daisies (*Bellis perennis*). Crouching low and quietly as they fed, their green upperparts blending with their surroundings, they were easily overlooked. We also became accustomed to seeing finches foraging on the greens about colonies of Gentoo Penguins (*Pygoscelis papua*) or on greens that paralleled the coasts or carpeted the valleys.

By early December, as the nesting season wanes and more broods fledge, flocks of finches begin building up until, by late January, practically all finches are in flocks of varying sizes. On six field trips to Cape Pembroke, the first on 31 March 1972 and the last on 6 August, Booth (pers commun.) saw flocks of from four or five individuals up to as many as 100. He first noted finches in pairs, 20 and 27 August, and in pairs that appeared to be establishing territories, 10 September. Between breeding seasons, Woods (pers. commun.) observed numerous flocks, usually from 10 to 40 individuals. The largest, of about 1,000, was spread along the dunes at York Bay, 30 May 1957, the birds calling and singing incessantly.

## BLACK-CHINNED SISKIN

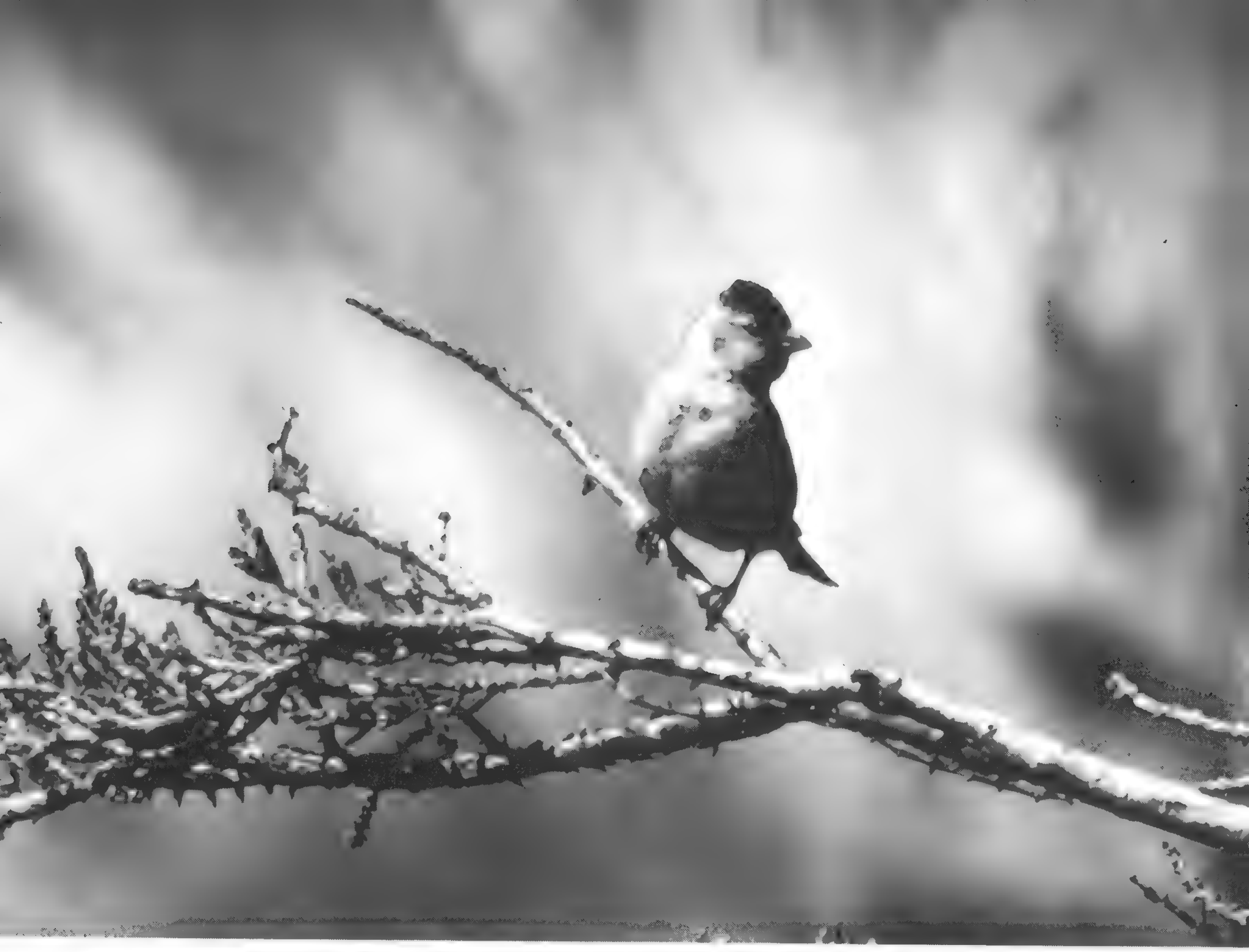
(Figures 14 and 15)

*Status.* — Common resident where tussock grass flourishes or where high, shrubby vegetation is native or introduced; consequently prevalent on tussock islands and in plantations of macrocarpa, gorse, and other woody growth about settlements. Nesting season: September through December.

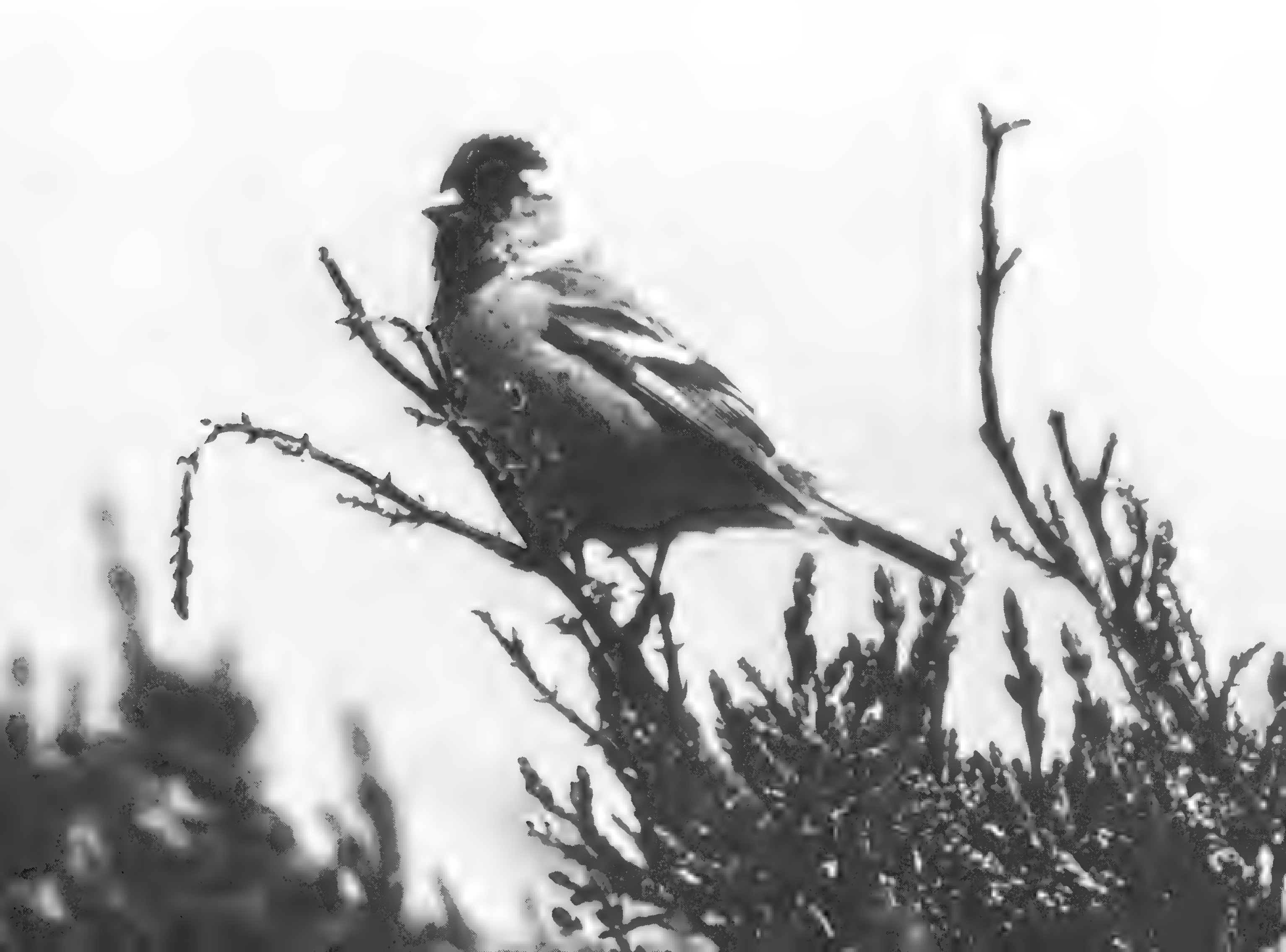
*Observations.* — We first encountered Black-chinned Siskins at Kidney Island on 4 November 1953. At this time there were several flocks, each composed of 10 to 12 males and females. The males were giving their full song — a long series of musical trills, distinctly canary-like, usually while perched on blades of tussock. We noted no singing in flight although the flocks, bounding through the air from one part of the island to the other, were always noisy, producing *cheeep* notes and various other short vocalizations. The call we most commonly heard was a *cheee-eep* with a rising inflection. Frequently this helped us in locating the birds which were so often, especially on windy days, deep in the tussock grass and obscured by their matching coloration.

By 7 November, the flocks had broken up in pairs. One remained in the tall tussock grass around the hut; the male was in full song and attentive to the female. Though we did not find the nest of that pair or of any other on the island, Woods (1970:21; pers. commun.) found one, 20 November 1961, about six feet above ground on the side of a tussock clump about halfway in toward the center from the tips of the tussock blades. Constructed entirely of tussock root fibers, very deeply cupped, and rather exposed, it held two nearly fledged nestlings.

Siskins were rare in Stanley and we missed seeing them until 24 November when we found a nest with two eggs four feet above the ground in a macrocarpa in Government Forest. The female, by responding to the male as he came to feed her on the nest, led to the discovery. She laid three more white eggs in the next three days until there were five on the morning of 27 November. During this period she was on the nest each time we arrived. On 25 and 26 November, we watched her being fed by the male at regular intervals while we stood nearby. At the end of each feeding, she



Figures 14 and 15 (*above* and *below*). Black-chinned Siskin perching on a macrocarpa in a ravine on West Point Island. The macrocarpa, or Monterey cypress, survives and grows, albeit slowly, when planted and cared for in the settlements. Its thickly foliaged branches provide shelter and nesting sites for siskins as well as for Austral Thrushes.



left the nest to follow her mate, then soon returned by herself to cover the eggs. Edwin Cawkell reported to me that three eggs hatched on 10 December. The other two eggs had disappeared mysteriously prior to this date. The incubation period was approximately 14 days. Surprisingly, the three eggs hatched at about the same time despite the fact that the female apparently had begun to incubate before the clutch was complete. The nest, saddled on a branch of the macrocarpa, was walled thickly and compactly with grasses and wool and lined with more wool and, in addition, horsehair.

Eighteen years later in Stanley, we were impressed by a marked increase in the population of siskins. We saw them around the many fenced-in gardens, often in noisy flight from one to another. On 26 November 1971, we found a nest in Government Forest as we had before. It was in a macrocarpa, 10 feet above the ground, with a single nestling ready to fledge. Our clue to the location of the nest was the pair of adults excitedly protesting a cat near the base of the tree. Like the nest found in 1953, it was saddled on a branch. The walls of the cup, nearly two inches thick, were constructed of macrocarpa twigs, mosses, fern leaves, bits of wool, and various unidentified plant fibers; the interior of the cup was lined with many chicken and goose feathers — probably from a nearby poultry yard — and wool.

In the settlements where we stayed for any length of time in 1971–1972 — at Port San Carlos, Fox Bay East, New Island, and West Point Island — siskins were numerous and conspicuous. At West Point Island, 13 December 1971, we found four nests in a nearby plantation of macrocarpa, other trees, and shrubs. Two were in macrocarpa, one in a pine, and one in a tall fuschia. All were empty, an indication that the nesting season was over.

According to Robin Woods (pers. commun.), siskins nest earlier than our observations indicate. He saw a pair building a nest in a macrocarpa in Government Forest as early as 2 September 1957. And he watched a female at Kidney Island, 29 October 1962, feeding a juvenile that was continuously soliciting her. The young bird must have come from an egg laid early in October.

Between breeding seasons, the siskins roved in small flocks about settlements. Woods (1970:21) saw no siskins at Kidney Island after late March and believed that they "move back to the main islands for the winter." Stuart Booth (pers. commun.) noted siskins repeatedly in Stanley during the winter of 1972, his attention often directed to them by their singing. Around homes sheltered by trees he observed frequent quarrels with House Sparrows, which were common.

Seeds were the only food that we saw siskins consuming. Seeds of the dandelion seemed to be favored whenever available. At Kidney Island, siskins avidly fed on the seeds of tussock grass and wild celery (*Apium graveolens*). The stomachs of three specimens that I collected on 17 February 1954 were full of green celery seeds. Woods (pers. commun.) saw a pair in a small clump of diddle-dee, possibly taking berries. In Stanley, he also watched a pair presumably feeding on the buds of a deciduous shrub.

*Remarks.* — Cawkell and Hamilton (1961:25) wrote that the distribution of the Black-chinned Siskin in the Falklands had changed considerably since the 1920's. In the earlier days, the species was said to be common only on West Falkland and outlying islands where the one native shrub of any size was *Veronica elliptica*. With the decrease in this shrub through excessive grazing and the increase of other shrubs through planting about settlements in East Falkland, the species spread eastward accordingly. This may have accounted for the marked increase of Black-chinned Siskins that we noted in Stanley between 1953 and 1971. Whether tussock grass as a nesting habitat was a development subsequent to the selection of *Veronica*, and later the plantations of shrubs and trees, is a moot question. I am inclined to believe, as does Woods (pers. commun.), that tussock grass has always been a natural habitat of the Black-chinned Siskin and that the spread of the species has come about as much from the depletion of tussock grass as from the depletion of *Veronica*.

## *Discussion*

### Why Only Nine Native Passerine Birds?

In Tierra del Fuego, Humphrey *et al.* (1970) listed 39 passerine species of which 22 are *definitely* known to breed. These include the same species found in the Falklands except the Blackish Cinclodes (=Tussockbird). Five, including the Austral Thrush, inhabit forests or their edges; the others are ground-dwellers or at least occupants of open, sometimes brush-covered, sometimes mountainous, country much like that in the Falklands.

Many southern South American passerine birds reach the Falklands as vagrants, no doubt blown by the strongly prevailing westerly winds. Cawkell and Hamilton (1961) listed 12 passerine vagrants of which at least three — the White-crested Elaenia (*Elaenia albiceps*), Chilean Swallow (*Tachycineta leucopyga*), and Rufous-collared Sparrow (*Zonotrichia capensis*) — are among the breeding species listed by Humphrey *et al.* in Tierra del Fuego. During both our sojourns in the Falklands we observed swallows: in 1954, three Chilean Swallows on 13 February and one (collected) on 23 February at Kidney Island, another on 7 March at Cape Pembroke; in 1953, one Barn Swallow (*Hirundo rustica*) in Stanley on 28 December; and in 1971, one at Kidney Island on 12 November. The late J. E. Hamilton (pers. commun.) considered the Barn Swallow "irregular but frequent almost every year." Earlier in this article I mentioned two vagrant tyrannids observed, the Fire-eyed Diucon by Robin Woods in 1961 and the Fork-tailed Flycatcher by us in 1972.

Why nine species of South American passerines have become established while others have not defies full explanation. Climate, equable though cool the year round, can hardly be a preventive factor. The absence of forests may be an inhibiting factor although apparently not for the Austral Thrush. The most obvious factor, and perhaps the most important, is the paucity of insects upon which so many passerines depend for their own survival and/or for feeding their young. Certainly the paucity of flying insects is a detriment to flycatching birds such as swallows and most tyrannids.

### Distribution and Numbers of Passerine Birds

Anyone looking for birds in the Falklands is soon struck by the sparsity of passerines and other land birds on the white grass and diddle-dee heath

— the most extensive area and the natural habitat of the Correndera Pipit, Long-tailed Meadowlark, and Black-throated Finch. E. M. Cawkell (*in* M.A.R. Cawkell *et al.*, 1960:210) wrote: "One may ride for several hours and see nothing except a few pipits, a finch or two, . . ." Our experience was the same.

The sparsity cannot be attributed to sheep-farming. Sheep rarely graze white grass and diddle-dee because they find them unpalatable. Instead they graze either the finer plants between the clumps of white grass or the greens. Although some sheep farmers burn areas of diddle-dee to encourage grassy growth — an effort that too often results either in erosion of the soil or the invasion of undesirable plants (W. Davies, 1939:32–33; T. H. Davies *et al.*, 1971:7) — the areas they destroy are insignificant in total extent. In all likelihood, the sparsity of the three species can be attributed to natural factors in the environment, such as food supply, that operate against larger numbers of individual birds.

One sees the greatest numbers of passerine birds in association with the tussock islands and the human settlements. Tussock grass originally fringed the coasts of all the major islands. Some of the first Europeans to view the Falklands from the sea reported them well wooded — an understandable misconception since any area supporting mature tussock clumps does indeed appear tree-covered from a distance. Unfortunately, tussock grass was in the way of seal-hunters who burned it to gain better access to their quarry. Then later, because the plant is highly nutritious and delectable to livestock, it was overgrazed to its extirpation in all areas accessible to cattle and sheep. Kidney Island and the other small outlying islands, not grazed, are relics of the tussock fringe.

Tussock islands are the sole habitat of House Wrens, the principal habitat of Tussockbirds and Grass Wrens, and the natural area most frequented by Austral Thrushes. For these species they provide cover in every respect as protective as brush, marsh vegetation, and densely growing trees, a wide selection of nesting sites, and, owing to the natural proximity of tussock grass to the sea, a food supply enriched by an abundance of small arthropodal life on the shore. If Kidney Island — the tussock island that has received the most ornithological attention — is a relic truly representing the tussock fringe, we may assume that the present populations of the Tussockbird, the two wrens, and the Austral Thrush are mere fractions of the populations that once existed. Furthermore, we can readily understand why both the House Wren and the Austral Thrush — species ancestrally associated with brush and forest edge, respectively — so successfully established themselves in the Falklands.

Human settlements with their tree plantations and buildings, cultivated areas and closely cropped grass, and concentrations of domestic animals, including poultry, provide either shelter or food, directly or indirectly. Invariably, we saw more Dark-faced Ground-tyrants, Austral Thrushes, Long-tailed Meadowlarks, Black-throated Finches, and Black-chinned Siskins in the neighborhood of farm settlements than elsewhere. The prevalence of insects about woolsheds, poultry yards, and paddocks attracted ground-tyrants and meadowlarks. Additionally, gorse hedges were attractive to meadowlarks which used their tops for song perches and nested on the ground beneath them. To the thrushes, trees were an inducement for nesting, and the ground provided earthworms and beetle grubs for food. The finches apparently found the introduced grasses and other plants that comprised the swards of lawns and paddocks a source of small seeds, while the siskins were lured by the trees for nesting and the seeds and fruits of the garden shrubs and plants for food. Neither in Stanley nor in any of the settlements that we visited were the birds induced to the vicinity by feeding stations.

### Predation

In their belief that falconiform birds prey on lambs and raid poultry yards, many sheep-farmers have regularly shot all species. Thus, both the Red-backed Hawk and Peregrine Falcon, the only daytime predators likely to take passerine birds, are rare — too rare to have an appreciable effect on the passerine populations.

I did not see either species taking passerines. Cawkell and Hamilton (1961:25) spoke of the Peregrine preying on flocks of Long-tailed Meadowlarks. We frequently saw a Peregrine or two patrolling the beach at Kidney Island. At New Island, on days when the settlement was shrouded in fog, we often saw one or two Peregrines about the buildings and paddocks where we presumed, as did the Davises, that they were in quest of thrushes and meadowlarks.

At Kidney Island, the Short-eared Owls, which are noticeably active on storm-darkened days and near dusk, must take at least an occasional passerine, although our only evidence of the owls' avian quarry were the wings of the smaller petrels that we found on or between tussock clumps. Cawkell and Hamilton (1961:22) reported finding a Tussockbird skull in the pellet of a Short-eared Owl. The predation of this owl, the only owl species in the Falklands, is mainly on birds associated with tussock areas, its principal habitat.

The presence of cats or rats seems not to have a serious effect on the populations of ground-tyrants, thrushes, meadowlarks, finches, and siskins if we may judge by the prevalence of these species about settlements. It is possible, however, that cats or rats may account for the restricted distribution of the House Wren and Tussockbird. Woods (pers. commun.) contends that the presence or absence of cats or rats is as important as the presence or absence of tussock grass in determining the distribution of the Tussockbird. He believes that, without these human symbionts, the Tussockbird would occur more frequently away from tussock grass — just as it does on Carcass Island where both cats and rats have been effectively controlled.

### Length of Nesting Season

Even though the Falkland climate is equable the year round, the nesting season is generally confined to three or four months, from September or October through December or January. The Tussockbird, Austral Thrush, Correndera Pipit, Long-tailed Meadowlark, and Black-throated Finch have the longest nesting seasons. The thrush may rear two, or even three, broods (Cawkell and Hamilton, 1961:24), and we have evidence that the meadowlark may have two broods.

### Local Movements

The Tussockbird and the two wrens are clearly sedentary, staying in, or close to, their habitats the year round. Ground-tyrants, after the nesting season, tend to wander in small numbers, presumably family groups, as suggested by Cawkell and Hamilton (1961:22). The other five species, after the nesting season, gather in flocks of varying sizes and travel afar in the Falklands, often visiting situations quite different from their accustomed habitats.

Despite some suggestions of migratory activity in the Correndera Pipit, there is no substantiated evidence that any of the five species leaves the Falklands for South America. And there are at least two good reasons to support the belief that they remain. The winter climate is not severe enough to induce migration. The strong and incessant winds from the west operate against migration by making hazardous — and therefore highly improbable — any flight across the 300–400 miles of open ocean to the South American mainland. Thus, the winds that we assume brought the species to the Falklands in the first place are the same winds that keep them there.

## *Summary*

In the Falkland Islands there are nine native passerine bird species: the Blackish Cinclodes or Tussockbird (*Cinclodes antarcticus*), Dark-faced Ground-tyrant (*Muscisaxicola macloviana*), Grass Wren (*Cistothorus platensis*), House Wren (*Troglodytes aedon*), Austral Thrush (*Turdus falcklandii*), Correndera Pipit (*Anthus correndera*), Long-tailed Meadowlark (*Sturnella loyca*), Black-throated Finch (*Melanodera melanodera*), and Black-chinned Siskin (*Spinus barbatus*).

I have given an account of each of these species as observed by Mrs. Pettingill and me during two austral springs and succeeding summers. In each account I described our impressions of behavior, including vocalizations, presented nesting data obtained by ourselves and others, and contributed information of feeding habits and post-nesting activities. I also stressed the relationships of the species to the Falkland environment — geographical features, climate and weather, human settlement and industry, vegetation, and animal life — described briefly in the beginning of this article. On the basis of information published on the same species in South America, I attempted to compare the behavior and ecology of the populations in the Falklands with those in South America.

In my discussion following the species accounts, I conclude that the sparsity of breeding species in the Falklands is due to the paucity of insect food. The populations of native passerines are sparse in all areas of the Falklands except on tussock islands and about human settlements. Although there are two falconiform birds and one owl that are the most likely avian predators on passerine birds, the falconiform birds are too rare to have an appreciable effect on passerines while the owl is a predator mainly associated with tussock areas. The nesting season for passerines is confined to three or four months despite a remarkably equable year-round climate that would seem to permit a longer season. There is no substantiated evidence of passerines migrating to the South American mainland.

## *Acknowledgments*

Mrs. Pettingill and I worked in the Falklands during 1953–1954 under the auspices of Walt Disney Productions. My work in 1971–1972 was supported in part by a research grant from the National Geographic Society.

During both sojourns, our work would have been impossible without the assistance and many courtesies extended to us by numerous officials of the Falkland Islands Government and the Falkland Islands Company. Nor could we have proceeded without the thoughtful advice and generous hospitality of many people. In particular I acknowledge the following: In 1953–1954, Mr. Edwin M. Cawkell who planned much of our itinerary, arranged our field trips, and with Mrs. Cawkell hosted us in their home; the late Mr. Jack Davis and Mrs. Davis shared their New Island home with us and helped us immeasurably in sundry ways; and the late Dr. J. E. Hamilton of Stanley gave freely of his vast store of knowledge about birds gained from his thirty years in the Falklands. In 1971–1972, Mr. and Mrs. Roderick Napier of West Point Island, Mrs. Jack Davis and Mr. Raymond Davis of New Island, Mr. and Mrs. Alan Miller of Port San Carlos, and Mr. and Mrs. Richard Cockwell of Fox Bay East, in whose homes we were guests, provided us with every possible means of making our stays productive as well as highly enjoyable; the courtesies and accommodations of Mr. Osmund Smith of Johnson's Harbour made possible our work at Volunteer Beach; Mr. and Mrs. Desmond King, proprietors of the Upland Goose Hotel in Stanley, where we made our headquarters, went out of their way to ensure our comfort and facilitate our work in Stanley.

I am greatly indebted to Dr. Theodore H. Hubbell of the Museum of Zoology, University of Michigan, and the late Dr. Herbert B. Hungerford of the University of Kansas for the identification of insect specimens, and Dr. Rogers McVaugh of the Herbarium, University of Michigan, for the identification of plant specimens that I collected in 1953–1954; Mr. Donald McNaughton, formerly of the Meteorological Service in Stanley, for supplementing the climate and weather data from Brooks (1932), which I have used in this article, with his own summaries of the 1953–1954 summer season; Mr. Stuart Booth, a resident of Stanley since 1951, for giving me his notes on bird observations; Mr. Robin W. Woods for his nesting records and other notes obtained during his years in the Falklands from December 1956 to April 1963 and for his critical reading of the species accounts: and Dr. Milton W. Weller for his field notes obtained while he was conducting waterfowl studies in the Falklands from October 1970 to mid-January 1971.

My final acknowledgment of indebtedness goes to Mr. Maurice A. E. Rumboll of the Museo Argentino de Ciencias Naturales, Buenos Aires, who was my assistant in the sojourn of 1971–1972. His unfailing help, buoyant enthusiasm, and enduring companionship, in fair weather and foul and in the disappointments occasioned by failures in transportation, contributed in a large measure to the success of our work.

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# BREEDING BEHAVIOR OF THE SNOWY OWL

PHILIP S. TAYLOR

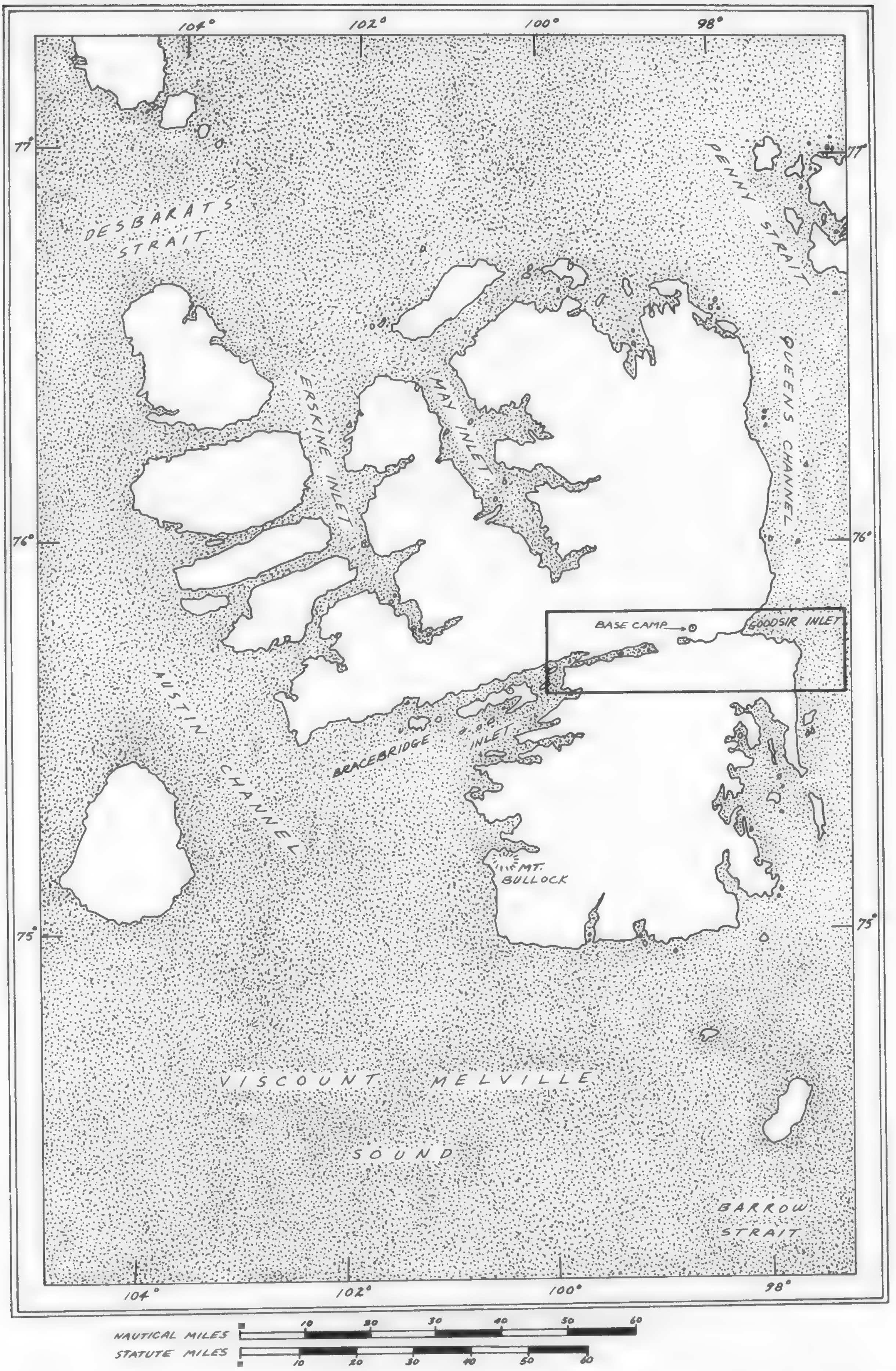
Drawings and photographs by the author

In its circumpolar distribution, the Snowy Owl (*Nyctea scandiaca*) breeds in both the high and low Arctic tundra regions. It is abundant during years of high lemming numbers and rare or absent when rodent populations decline. Irregular and sometimes spectacular winter flights of Snowy Owls to southern Canada, the northern United States, central Europe, southern Siberia and Mongolia (Bent, 1938: 370; Pleske, 1928: 165) may be a result of decreases in lemmings, its usual prey (Godfrey, 1966; Gross, 1947). Being diurnal and large in size, Snowy Owls are easily observed. All of these factors have contributed in generating much interest in this species and the scientific literature on Snowy Owls is correspondingly rich. Information on their breeding behavior beginning with incubation is fairly complete, and the several authors who have provided it and other aspects of breeding biology appear to agree closely on most aspects (Parmelee, 1972; Parmelee *et al,* 1967; Pitelka *et al,* 1955a and 1955b; Pleske, 1928; Sutton, 1932; Sutton and Parmelee, 1956; Tulloch, 1968; and Watson, 1957). However, we lack adequate descriptions of the courtship behavior of the Snowy Owls.

As field assistant to Stewart D. MacDonald, Curator of Vertebrate Ethology at the National Museum of Natural Sciences in Ottawa, Canada, I participated in the Museum expeditions to Bathurst Island, Northwest Territories during the summers of 1968, 1969, 1970, and 1971. In 1969, Snowy Owls bred in the vicinity of our base camp, allowing members of the party to make detailed observations on breeding behavior and ecology. The breeding of one pair of owls near camp in 1971 permitted us to confirm earlier observations. In this paper, I present some of my observations on the courtship behavior of Snowy Owls. Included are other behavioral observations, which add to the present information on these birds. I have outlined briefly the breeding cycle of the Snowy Owl on Bathurst Island, from arrival to departure, to place the courtship behaviors in proper temporal context.

## *Study Area*

Between Goodsir and Bracebridge Inlets (Figure 1) stretches a broad valley system, bordered on the north and south by gravel-strewn ridges rising


104°
102°
100°
98°
77°
77°
DESBARATS STRAIT
PENNY STRAIT
QUEENS CHANNEL
ERSKINE INLET
MAY INLET
76°
76°
BASE CAMP
GOODSIR INLET
AUSTIN CHANNEL
BRACEBRIDGE INLET
MT. BULLOCK
75°
75°
VISCOUNT MELVILLE SOUND
BARROW STRAIT
104°
102°
100°
98°
NAUTICAL MILES
10
20
30
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STATUTE MILES
10
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40
50
60

Figure 1. Map of Bathurst Island, Northwest Territories, Canada, showing the site of this study. Base camp is situated on a dry ridge on the north edge of a large valley between Goodsir and Bracebridge Inlets. Field work was carried on during the summers of 1968 through 1971.

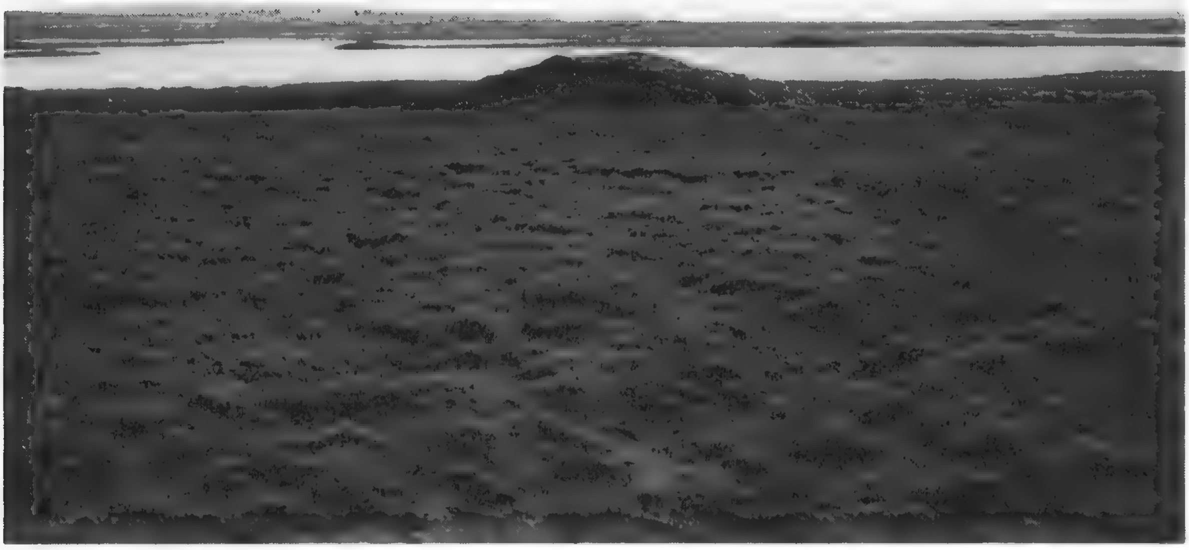
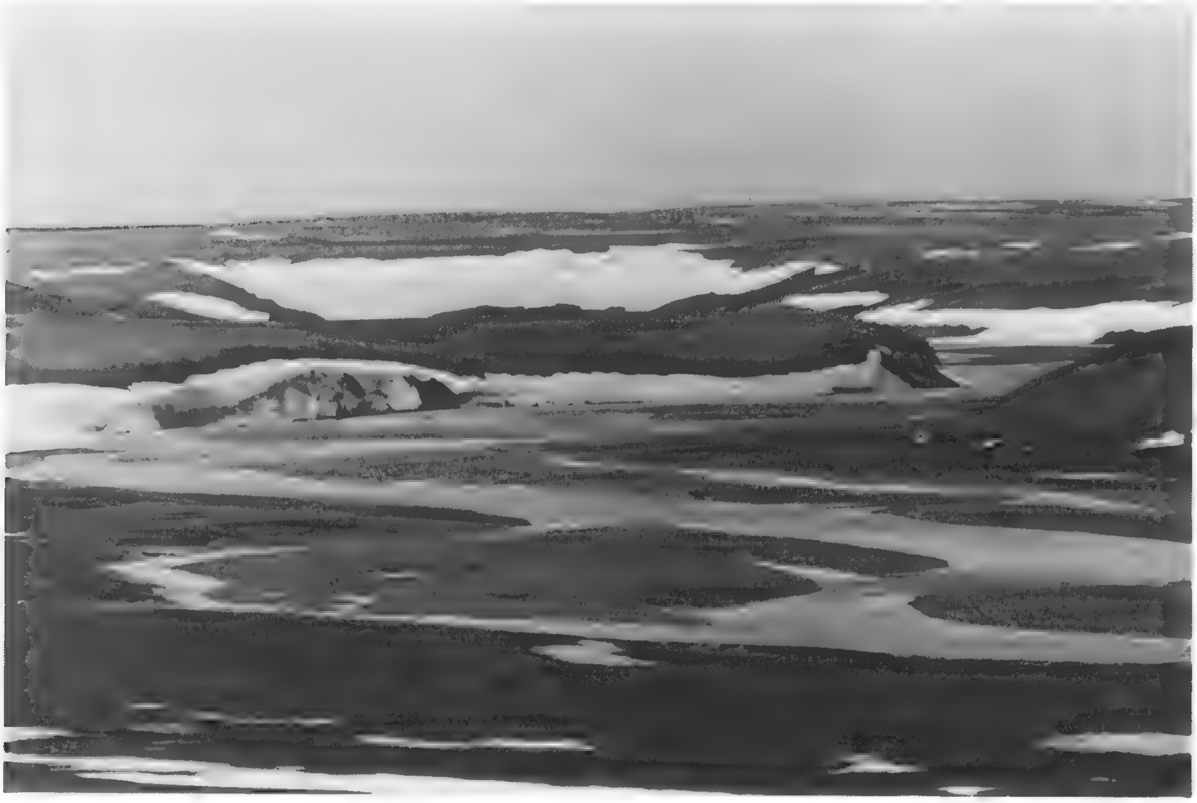


Figure 2 (*above*). A view of part of the wet and relatively well-vegetated valley bottom. Hummocks (foreground) are scattered throughout the area. Sedges, grasses, and mosses dominate the plant communities in the area. Photograph by the author.

Figure 3 (*below*). A view of the dry ridges which bound the valley on the north and south. Willow, saxifrages and *Dryas* commonly grow on these drier sites. Photograph by David R. Gray.



approximately 80 to 160 feet above the valley floor. Numerous lakes, ponds, and marshy sedge-meadows cover much of the valley bottom (Figure 2). Hundreds of well-vegetated frost mounds, ranging up to 10 feet in height, exist throughout the valleys and along stream courses farther into the hills. Rocky outcrops are scattered throughout the barren ridges and hills (Figure 3). Base camp is located on one ridge, which projects out into the main valley. Snowy Owls utilized both the valley and ridge systems for breeding in 1969.

### *Methods*

With 24-hour daylight prevailing during the entire field season in 1969, I was able to observe Snowy Owls at any time of the day. During April, May, and much of June, only overcast or "white-out" conditions and windy days with ground drifting snow resulted in such poor contrast between the owls and the snow as to make observing impossible. Usually, visibility was excellent throughout the season. The low ridges provided good locations for watching owls in the valleys or on neighboring hills.

I made most of my observations on owls within three or four miles of camp, although I also found pairs of owls farther from camp. I saw the behavior patterns frequently and made notes and pencil sketches of the display sequences while in the field. I watched most activities within a distance of four hundred yards. By using a spotting scope with 15X, 25X and 40X eyepieces, and 7 × 35 binoculars, I could see details of the behaviors without appearing to disturb the birds. The drawings in this paper are made from field sketches and, when possible, from photographs.

I spent 31.5 hours in a blind at one owl nest from 13 June to 20 July in 1969. Here I could photograph the birds more easily.

The darker markings and larger size of female Snowy Owls allowed me to readily distinguish them from the males.

## *Summary of the Breeding Cycle*

Snowy Owls arrive on Bathurst Island when the tundra is still snowbound. I saw a few individuals perched on rocky eminences and large mounds as early as 30 April in 1969 (males and females). In 1970, we recorded the first owl, a female, on 4 May, although fresh pellets and droppings found on 1 May indicated that birds arrived in the area earlier. David R. Gray and Don Cockerton observed a lone female in the vicinity of camp on 27 February and 8 March in 1971 when there was less than 12 hours of daylight. In 1969, I saw one bird flying in protracted flight at a height of some one hundred feet over the tundra in early May. It alternated flapping (about eight seconds) with sailing (three to five seconds) and was probably migrating.

Snowy Owls begin courting in early May (described in detail below). Pairs are scattered unevenly over the tundra and are thought by most authors to be territorial (Parmelee *et al*, 1967; Watson, 1957). Ridge tops, rock outcrops, and mounds are the only areas suitably free of snow in May and early June for the owls to nest. I accidentally flushed one female from a clutch of four eggs during a blizzard on 29 May 1969. Snow had drifted to a depth of four inches immediately about her. She deserted. All other nest sites remained essentially snow-free and no other females deserted, even if flushed. These sites also have a commanding view of the surrounding tundra (Figure 4). With the first egg laid, usually in late May or early June, the female begins incubation (32 to 33 days per egg). At this time, the females are amazingly well camouflaged; their darkly flecked plumage often

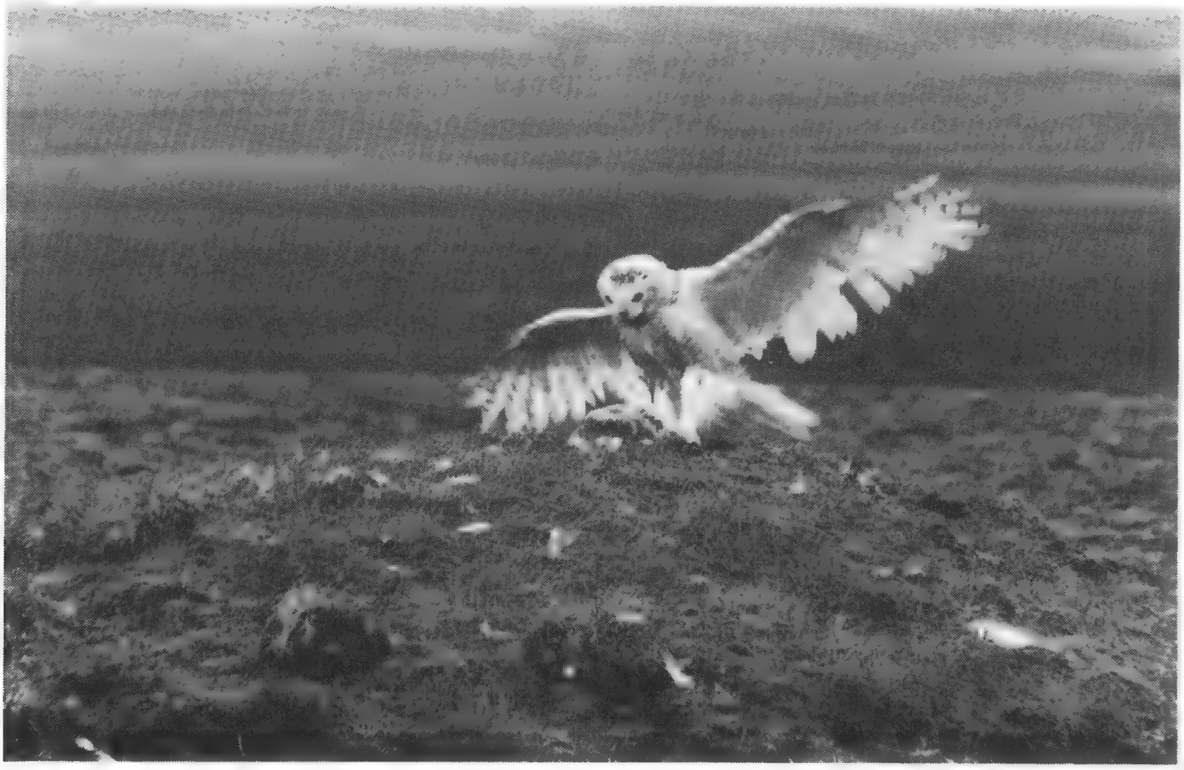


Figure 4. Female Snowy Owl landing on her nest hummock. Ragged plumage and strewn feathers are evidence of the molt which adults undergo while nesting. The young owls sit quietly in the nest cup. Photograph by the author.

closely resembles the snow-dusted, grassy hummock or outcrop on which they nest. Females initiate their clutches at different times. The variable size of the clutch (three to nine eggs) results in considerable asynchrony in incubation, hatching (Figure 5), fledging, and other related events (Figure 6). This is typical of Snowy Owls (Pleske, 1928:166). The male feeds his brooding mate on the nest. When about sixteen days of age, the young leave the nest to scatter over the nearby tundra where the male feeds them. When all have left, both parents attend the brood until all young are fledged—some 45 to 50 days after hatching (Parmelee *et al*, 1967). Throughout nesting, the male actively defends the eggs and young against enemies, even wolves and Arctic foxes. Wet cold weather, starvation, and cannibalism are probably responsible for most of the mortality in young owls (Parmelee *et al*, 1967).

The departure dates of Snowy Owls from Bathurst Island are incomplete because few observers have remained after August. We recorded birds regularly to the end of August in the years 1968–1971. One dark bird, seen on 23 September 1970 by Gray and Cockerton, who remained through that year, may have been an adult female or a juvenile.

## *Courtship Behavior*

### Aerial Display

Tulloch (1968), in describing the behavior of a Snowy Owl after it had chased an intruding owl out of its territory, stated that the male "occasionally flew back to the female with a special flight to perform displacement coition." Later, he described this flight of the male as having "exaggerated wing-beats, especially on the upstroke, so that his body went markedly up and down at each beat; on the up-stroke the wings were momentarily held almost vertically." A male owl described by Sutton (1932: 206) as flying "stiffly" was probably using this flight display. Watson (1957) saw "displacement coition" in Snowy Owls "over a hundred times" in the summer of 1955, but did not describe this special flight. In 1969, I observed this display on Bathurst Island in a more complete form and not purely as a "displacement activity."

From 2 May to 19 July, I saw male Snowy Owls using a display flight that was most complete and predictable early in the year. In May and the first three weeks of June, I saw it commonly. They flew with a marked delay in each wing beat at the top of the exaggerated stroke, which caused the body to sink one to two feet depending upon the duration of each stall. With rapid power and recovery strokes of the wings, the bird regained the lost height, then held the wings again in the high "V" position over its back (Figure 7), thus progressing in an undulating fashion. Toward the end of the flight, the male gradually climbed in altitude, usually about five to ten feet, whereupon it either set its wings in a "V" and sank gently to the tundra (reminding me of the attitude adopted by Rock Doves, *Columbia livia,* as they sail toward a perch), or flapped during the almost vertical descent (Figure 8). I did not hear the birds vocalize during this display. Displaying owls were visible from considerable distances and, when seen from afar, gave the impression of a large white moth flying over the tundra.

In early May, the males commonly initiated the display flight when a female was perched, even if she were half a mile away. The flight was oriented toward, away from, or past the female. The length of each display flight often depended upon the distance separating exposed areas, varying from nearly one mile to only a few dozen yards. Females on the wing, showing no exaggerated flight pattern, also could elicit this display behavior from the male. Females were invariably in evidence when males performed the aerial display. By June, most pairs had clutches, warmer temperatures exposed more tundra and hummocks, and the display flights were shorter.

In May, I could usually see a lemming (*Dicrostonyx groenlandicus*) in the male owl's bill as it displayed. Later, in June and July, the birds carried lemmings only infrequently while displaying.

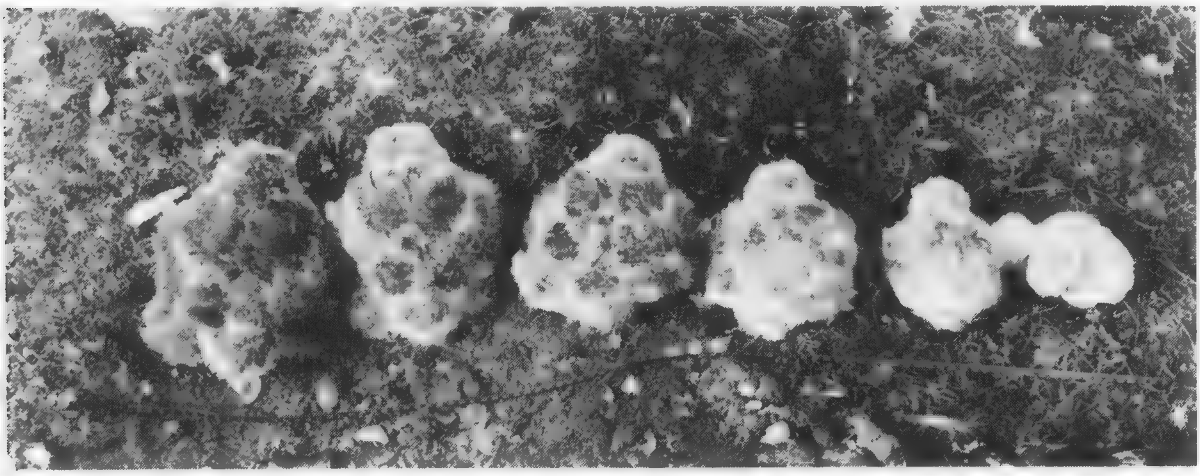


Figure 5. Incubation begins with the laying of the Snowy Owl's first egg. This results in a staggered hatching of the eggs and great size variation between siblings. Pictured here are the young produced by one pair of owls that bred on Bathurst Island in 1969. The nest hummock and nest cup, in the lower part of the picture, contain pellets cast by the owls. Photograph by the author.

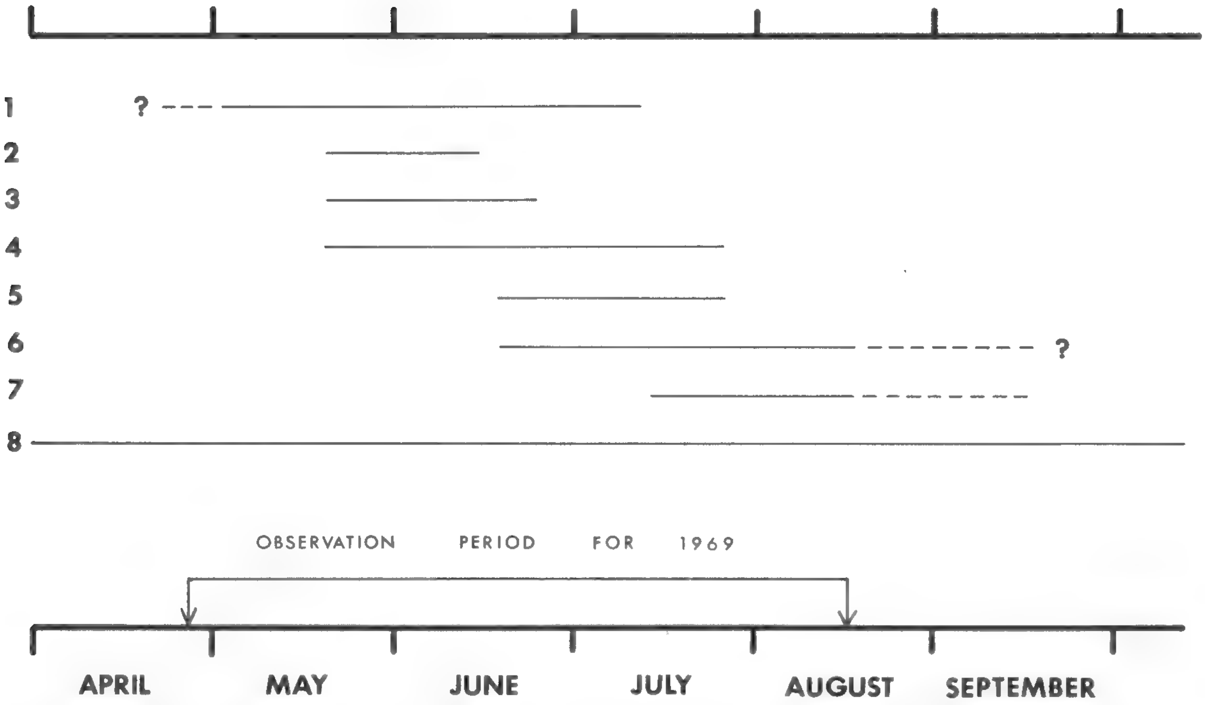


Figure 6. Generalized chronology of the nesting Snowy Owl population on Bathurst Island, 1969. Numbers on the diagram indicate the following: (1) pairing and courtship behavior, (2) clutch-initiation, (3) egg-laying, (4) incubation, (5) egg-hatching, (6) young dependent upon adults — nestlings, (7) young out of the nests — fledglings, (8) Snowy Owls observed on Bathurst Island. Early phases of breeding must be initiated while snow is still covering the ground in order to complete the long breeding cycle before winter.

## Ground Display

Upon landing at the termination of an Aerial Display, the male usually began a ground display which formed the second part of the courtship displays I saw on Bathurst Island. Watson (1957) saw this phase of the display sequence only after coition, subsequent to human interference. He states that "twice a male after coition, stood leaning forward, wings half extended and tail rising up and down for a quarter of a minute." Pitelka *et al* (1955a) described a "pairing display" seen on two occasions in which the male landed fifty feet in front of the female carrying what appeared to be a lemming in its bill. The female "flew immediately to it, perching behind it. The white owl stood with its wings raised and leaning forward about one minute. Then it turned to one side maintaining the raised wing attitude. The brown owl stood quietly." These observations were apparently made on undisturbed birds. In 1969, I saw this display commonly in May, infrequently in June, and on only two days in July.

The sites used for the ground display were usually free of snow, elevated, and provided good visibility for the birds. It is, therefore, not surprising that ground displays took place in old nest scrapes, as we observed in 1969. Males displayed only when a female was in sight, and initiated some ground displays without a preceding aerial display. The transition from alighting with wings held in a "V" to the ground display posture was smooth.

Upon landing, the male owl often dropped the lemming it carried, leaving it on the ground while displaying. On May 16, I surprised a displaying male on a mound, and it flushed carrying something in its bill. I found

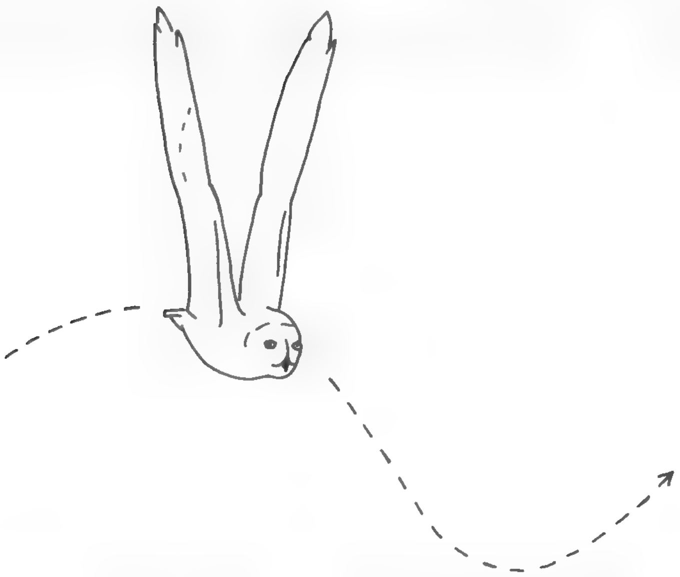
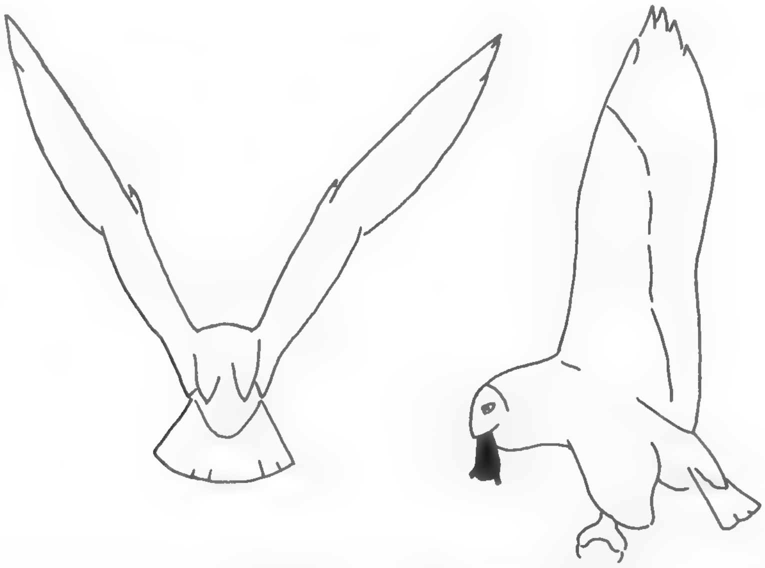


Figure 7 (*above*). The aerial display used by male Snowy Owls in courtship consists of an undulating flight over the tundra. Pictured is the attitude of the male at the point of delaying the wing beat which results in his sinking before the next wing beat. A lemming is usually carried during this display but was omitted from this drawing for clarity.

Figure 8 (*below*). The aerial display ends in a gentle vertical descent to the ground. The wings may or may not be flapped. Rear and side views of the male are presented. Note the lemming in the bill of the male. The aerial display is easily visible from a considerable distance.



feathers from the tail and wings of a Snow Bunting (*Plectrophenax nivalis*) on the mound, indicating that the bunting had been used in place of a lemming.

At the beginning of the ground display, the male remained fairly erect, keeping its wings partly spread with the wrists high (Figure 9). While displaying, some birds walked and turned slowly around within a few feet of the starting point, commonly orienting their back or sides, seldom their front, toward the female. As the display continued, the male leaned farther forward (Figure 10) with head lowered and tail partly fanned. I saw little tail movement, and each bird maintained a rather stiff overall appearance. Males frequently peered around their wings in the direction of the female being solicited (Figure 11A). The flat surfaces of the raised wings serve to reflect light which, as the bird turned, caused a flashing effect that was often visible for well over a mile. The wings stood out so markedly that on one occasion I mistook a courting male for two Arctic hares (*Lepus arcticus*). The female often flew toward the male at about this time and landed near him, sometimes immediately behind him. The female usually hopped closer to the male, perhaps begging for food. I heard no vocalization by the male or female at this time. Invariably, the male kept his wings up, leaned farther forward, and oriented his back or side to the female, as if in an effort to hide the lemming from her view. The wing closest to her was usually highest (Figure 11B). In an aerial display, the male soon flew to a new perch where he repeated the courtship posturing. If the female did not approach, the male moved to still another display perch. The ground display normally lasted only one or two minutes at each site, but one sequence continued for approximately five minutes.

I saw Snowy Owls using the aerial and ground displays during both the early phases of their courtship and incubation. On 6 May, one pair courted for over 30 minutes with no copulation ensuing. The male used both displays almost continuously and the female followed from mound to mound. I believe that a nest found later in the immediate area belonged to this pair. On 25 May, a female flew away from a mound, followed by a male, which executed an aerial display rather poorly. The male landed behind the female, appeared to mount, without becoming completely airborn, and copulated with her. On 30 May, a female left her nest for no apparent reason, whereupon the male some five hundred yards away immediately began a ground display. I consider these observations typical of undisturbed owls.

In June and, more rarely, in July, while visiting the owl nests, I saw the male perform both aerial and ground displays. Usually, I disturbed the female when one-quarter to one-half mile away from the nest, whereupon it flew 100 to 200 yards, occasionally half a mile. Courtship by the male owl began with one of the displays, either while the female was in flight or after it had landed. Once perched, the female assumed a copulatory posture: tail partly raised, wings held loosely at her sides, and leaning fairly far forward with body feathers generally slightly ruffled (Figure 12). Other writers, including Sutton and Parmelee (1956), Tulloch (1968), and Watson (1957),

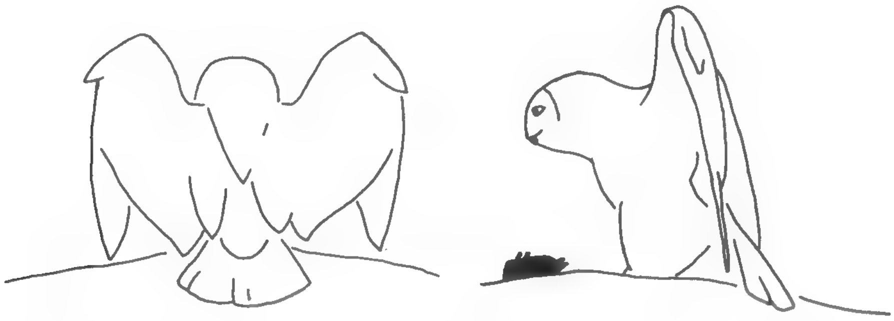


Figure 9. A second display used by the male Snowy Owl during courtship occurs on the ground. The early stage of a ground display is shown from the rear and side. The posture is fairly erect. The owl may slowly turn or walk about on the ground carrying the lemming in his bill. Light reflected off the flat surfaces of the wings is visible at great distances.

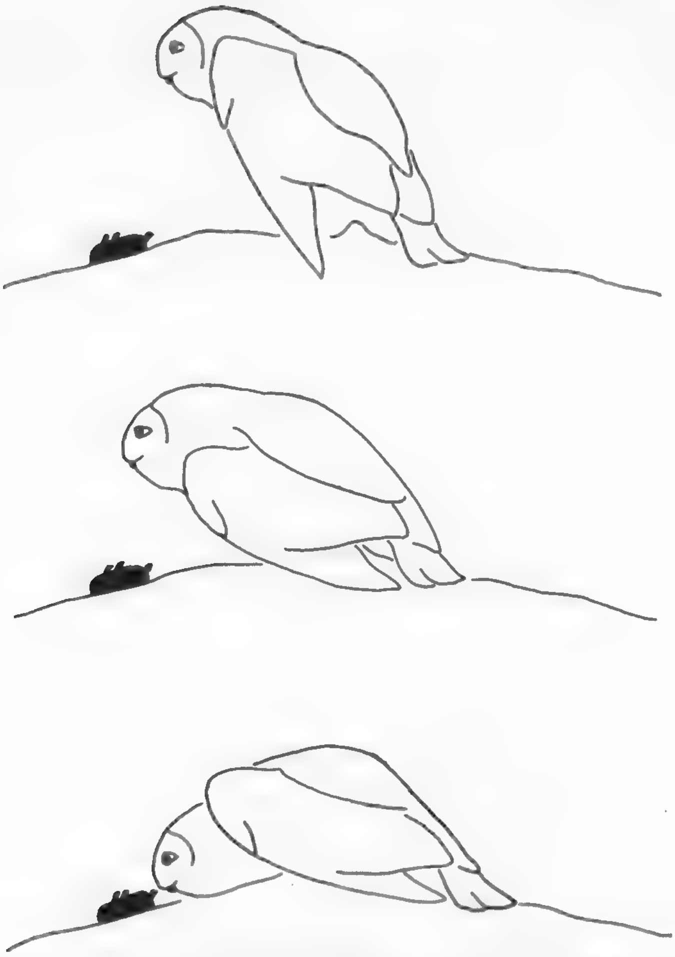


Figure 10. Transition from upright stance to lower stance in the ground display. When this posture is adopted, it frequently signals the closer approach of the female owl. A lemming is in front of the male.

have described this attitude of the female, which it maintains during copulation and for a brief period of time following. After copulation, some males continued to display. The aerial display was common and most complete while the female maintained the copulatory display. When I was closer to the nest, the male left the female and either attacked me repeatedly or perched nearby and gave a threat call until I withdrew.

On 21 June, while sitting in the blind, I flushed the incubating female from her nest. The male, which could not react directly to my presence, attempted to copulate with the female in a manner similar to copulations I saw when approaching a nesting territory. Then the female, uttering high, thin, squealing whistles, followed the male from mound to mound as he continued displaying. These vocalizations may or may not be a regular part of the following-response during courtship.

Only once did I see these displays by the male owl in any other context. On 16 July, Male 3 landed unusually close (125 yards) to Male 7 of an adjacent territory. The latter started a ground display that lasted only about ten seconds. Some minutes later one male, then the other, flew back farther into their own territories. However, little over an hour later, Male 3 returned to the same hummock and within ten minutes Male 7 also flew to the hummock that it occupied earlier. Male 7 rose in an aerial display, then commenced a ground display that lasted less than a minute. Interpretation of this situation is difficult, since I saw it only once. Only further observations will determine whether or not this behavior is used regularly in such

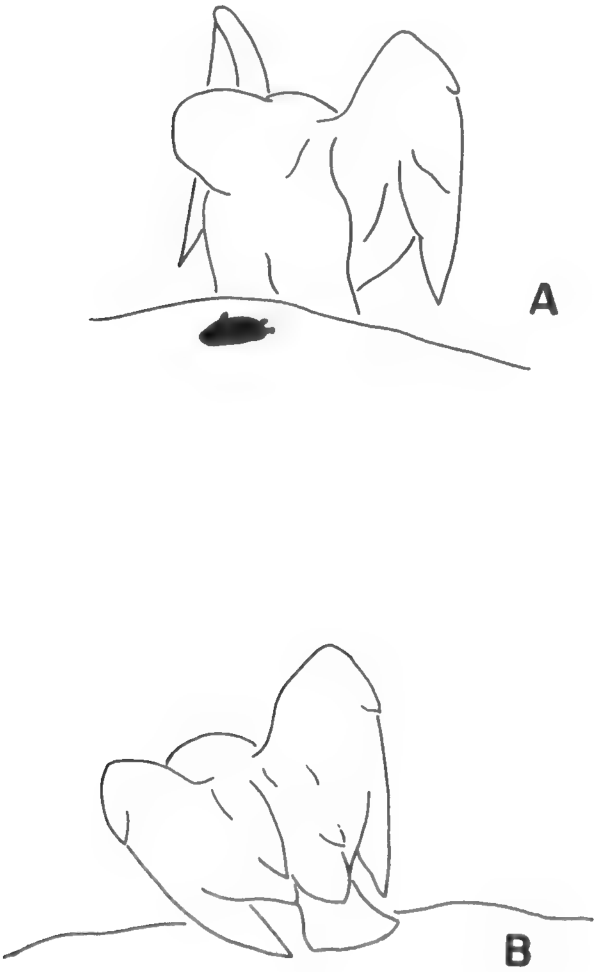


Figure 11. A displaying male looking back toward the female (A). The use of a lemming in courtship displays may indicate the presence of sufficient food for successful breeding by the owls. B shows late stages of male's ground display with the wing nearest the female held highest. The female has landed to the right of the male. Hiding the lemming from the female's view during courtship may be a ritualization of the attitude adopted by raptors on a fresh kill.

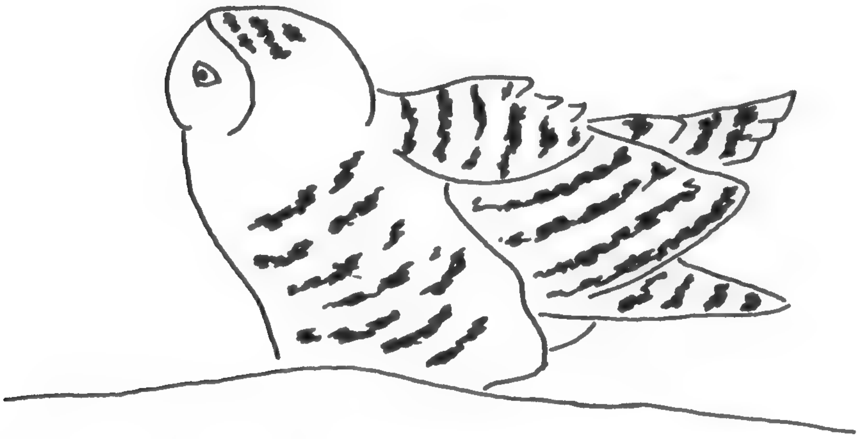


Figure 12. Copulatory display of the female adopted before copulation and continued through and after a copulation.

situations, particularly early in the year. If so, it may be of importance in establishing and maintaining territories.

I do not know the fate of the lemming carried by the male owl during courtship. Further study may reveal that the lemming is fed to the female, probably just prior to copulation. Courtship feeding is known to occur in other owls (Welty, 1962).

## Hooting

My 1969 observations indicated that the Territorial, or "song," Hooting Dislay of the male Snowy Owl is similar to that of the Great Horned Owl (*Bubo virginianus*) and that hooting volume is loudest in the context of territorial defense (Figure 13), confirming the work by Sutton (1932: 206) and Watson (1957). In May, I heard hooting at all times of the day and frequently from distances exceeding two miles. I heard no Territorial Hooting after 19 June. In 1970, I heard Territorial Hooting once in late June, by a male that had earlier performed an aerial display. I found no nest.

Male owls hooted from the ground when a human intruder entered their nesting territory at any time through the summer. The bird's posture while Threat Hooting was more upright in attitude and lacked the lifted

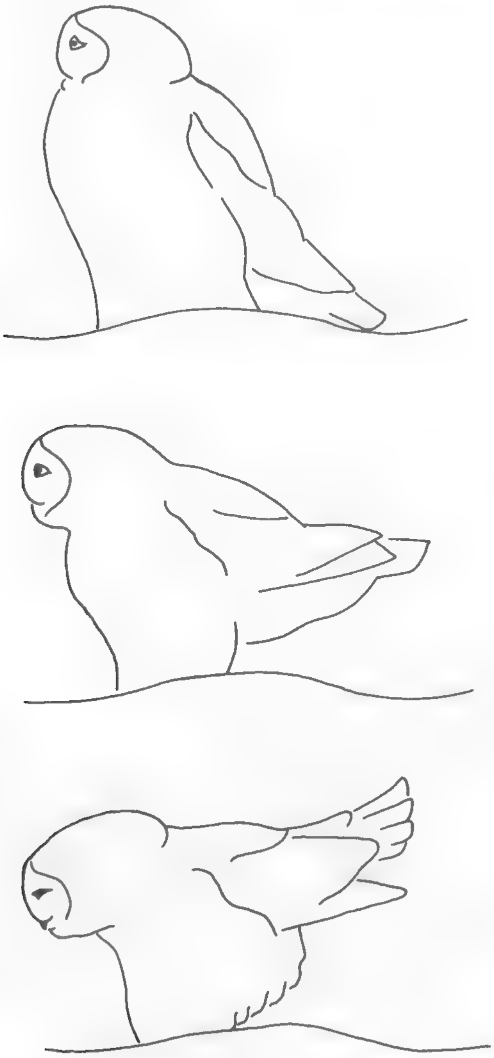


Figure 13. Attitudes of the male Snowy Owl during Territorial Hooting in May and early June: (a) male perched before and after hooting; (b) male pausing between hooting series; (c) male hooting. Hooting males can be heard from distances exceeding two miles.

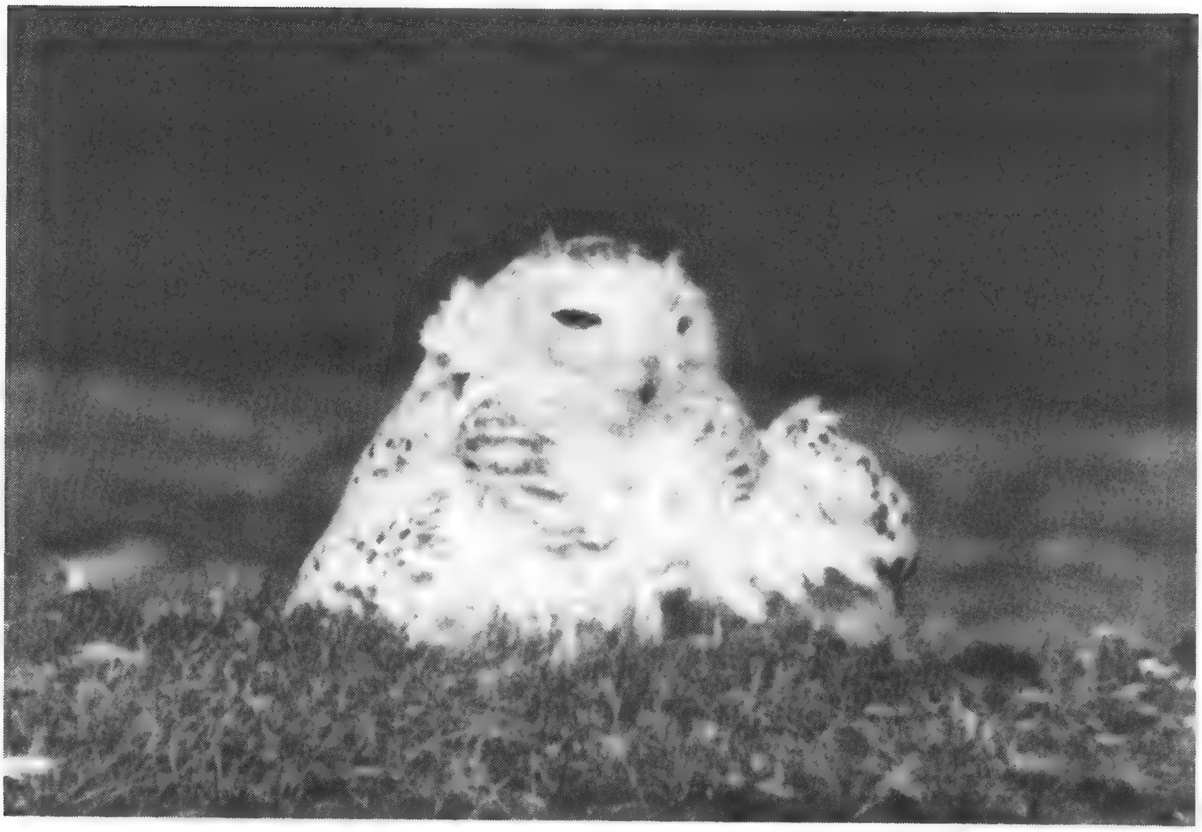


Figure 14. Female Snowy Owl incubating. Horns show when contour feathers are sleeked. The dark brown to black flecking of the female's plumage is remarkably cryptic during incubation and particularly so when there is a light dusting of snow on the ground. Photograph by the author.

tail of Territorial Hooting. I saw males occasionally hoot on the wing. It was always quieter than Territorial Hooting and most often took place as a response to my intrusion.

## *Incubation Behavior*

My observations from a blind near one nest corroborated the existing literature on behavior of Snowy Owls during incubation and brooding. The most complete description of behavior at the nest is given by Tulloch (1968), and I can add little to supplement his descriptions.

Toward the end of incubation, the female on the nest became more and more intermittent in her incubation duties. When we visited the nest in May and June, she returned within a few minutes of our departure. On 20 July, however, she remained away from the nest for fully two hours after I checked it. This may contribute to some mortality of eggs and chicks, even though the already-hatched chicks provide heat to their siblings and the remaining eggs. Irregularity of incubation in Snowy Owls, particularly in the later stages, is discussed more fully by Parmelee *et al* (1967).

I saw feather tufts or horns on all incubating females that I observed closely (Figure 14), but only after the bird settled completely on the nest. The sleeking of the contour feathers of the head, as well as the body, while sitting on the nest, made the half-inch-high horns visible. Dement'ev *et al* (1966) and Gabrielson and Lincoln (1959) describe the presence of horns but do not mention their conspicuousness during incubation.

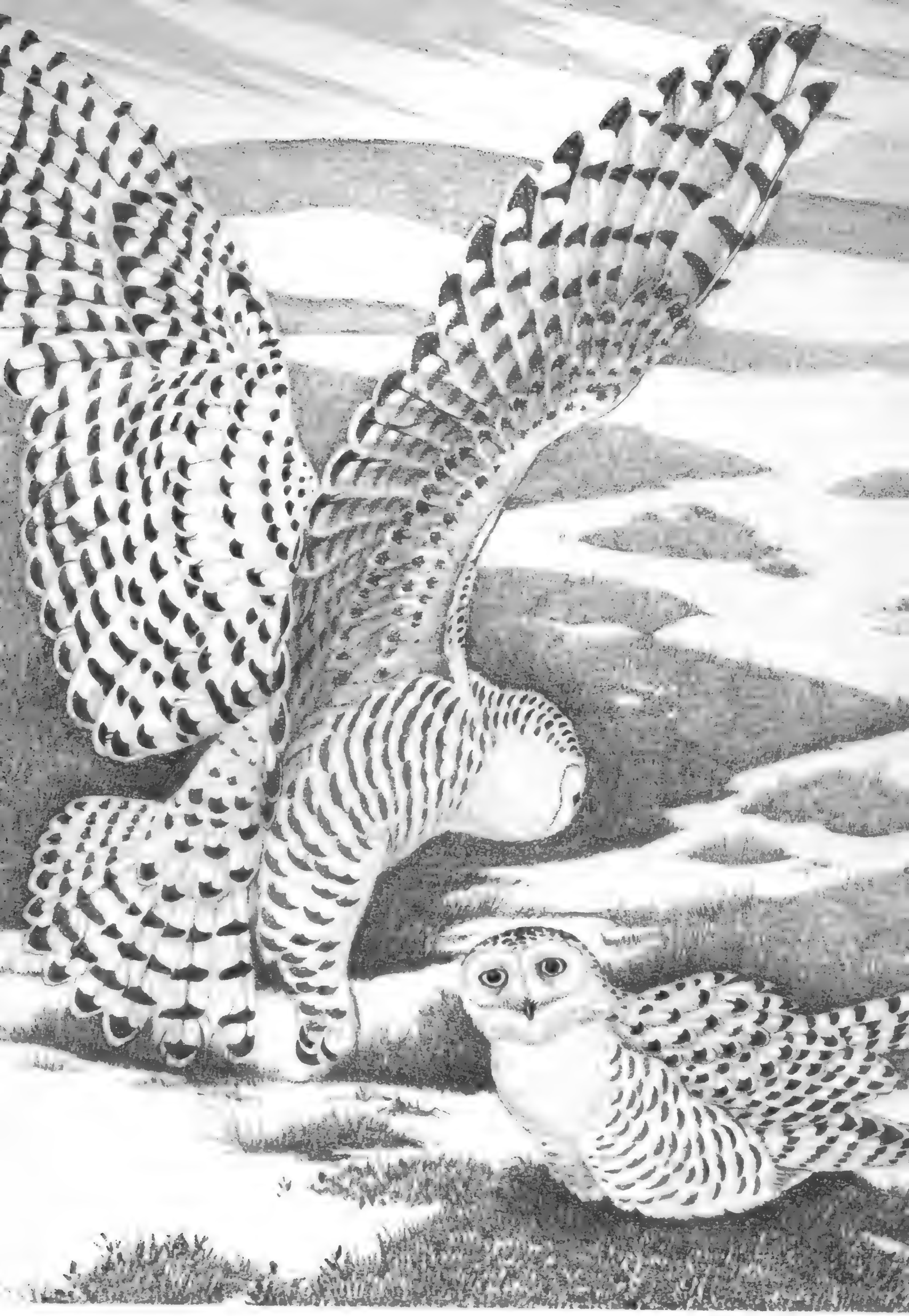
## *Discussion*

The aerial and ground displays in Snowy Owls function as long-range visual cues during courtship and show adaptations for both diurnal activity and life in open regions, such as the treeless Arctic tundra. Work done on a wide variety of other species of birds (Welty, 1962) and many Arctic birds (Parmelee, 1970; Parmelee *et al,* 1967; MacDonald, 1970) documents flight and ground displays as being quite common.

Some of the behaviors I regard as part of the Snowy Owl's normal courtship are described as "displacement activities" in association with "displacement coition" by Watson (1957; and *in* Baird, 1953) and Tulloch (1968). Watson also interpreted other workers' observations of copulations as "displacement coition," since observers were in the area of the nest. Tulloch (1968) stated that the owls "appear to copulate though it was never confirmed that actual mating took place" and, as a result, called them "displacement activities." Perhaps these actions sometimes occur under stress and hence might warrant the label "displacement," but I believe they occur regularly as part of normal courtship.

The owl copulations and courtship displays which followed human disturbance in 1969 on Bathurst Island cannot conclusively be classed as displacement activities for a number of reasons. The copulations and accompanying displays did not appear markedly disoriented or confused and most were not noticeably shortened or hurried as is usual with displacement activities (Manning, 1967). Because copulations took place soon after the female flushed (it took me several minutes to reach the nesting area, where the male attacked me), or after I left the territory, there was ample time for the displays of both male and female as well as for copulation. Tulloch (1968) describes aerial displays and copulations seen repeatedly after intruders left the territory. Watson (1957) saw a ground display after a "displacement copulation." Both saw the female's copulatory display. All of this would seemingly indicate unhurried behavior sequences. Any incompleteness in these displays could be characteristically late in the breeding cycle, since I saw the displays executed most completely early in the breeding season.

Neither can these copulations and displays be considered irrelevant to the situation — a common characteristic of displacement activities (Hinde, 1970; Manning, 1967; and Tinbergen, 1953). The opportunity for copulation attempts appears to be limited. Females only infrequently leave the nest, since they alone incubate, are fed at the nest by the male, and begin incubating with the first egg. I saw no copulations at the nest in 1969 and it is not reported by other workers. Thus, the female's flight from the nest may be interpreted by the male owl as copulation soliciting. More copulations may increase the percentage of fertilized eggs; fertility rates in female birds of other species drop rapidly after the first week if the females are separated from the males (Sturkie, 1965; van Tienhoven, 1968; Welty, 1962). Laying time in Snowy Owls can last as long as 22 days (Parmelee *et al,* 1967). Hence, it would seem advantageous for Snowy Owls to copulate whenever the female leaves the nest. Tulloch's (1968) statement that "displacement coition" occurred "only in the early stages of incubation and seldom after completion of the clutch," would tend to support the contention that these copulations are functional rather than displacement behaviors. There-



Drawing of Snowy Owls by Diane Pierce.

fore, the use of the term "displacement" in describing these behaviors in the Snowy Owl seems inappropriate.

A hovering flight occasionally used by male owls when above intruders in the nesting territory was similar to hovering used while hunting. I do not regard this behavior as a displacement activity, although Watson (1957) and Tulloch (1968) describe it as such.

### Evolutionary Importance of Displaying with a Lemming

The fact that density of breeding Snowy Owls varies with the abundance of prey is well documented (Parmelee *et al,* 1967; Pitelka *et al,* 1955a and 1955b). The food supply must be great enough to hold the adult owls in the area, if breeding is to be attempted; but how Snowy Owls determine suitable levels of prey to allow breeding before the snow has melted is not precisely known. The ability of a male owl to catch enough food to feed himself, then to use prey for courting, and finally to supply the female and young at the nest, determines the success of breeding in a particular area. The lemmings used in courtship could be representative of the numbers of lemmings in the area and might serve as a general indicator of the sufficiency of the food supply for breeding. Thus, if a lemming is necessary in courtship displays for initial pair-bond formation and the success of early copulations, the expenditure of energy for egg-laying would be prevented in years of food shortage when lemmings could not be caught. Palmer (1941) states that lack of fish for the Common Tern's (*Sterna hirundo*) "fish flight" has a detrimental effect on the bird's courting behavior. Indeed, the Snowy Owl's clutch size might even be determined by the number of lemmings the male uses during courtship. Such a hypothesis would explain the adaptiveness of incorporating a lemming into the courtship displays.

That the lemming has an important food-related role in the courtship of Snowy Owls is supported by the posturing during the ground display, which resembles the attitude adopted by many predatory birds on a fresh kill (wings and tail partly fanned while crouching low over the prey). This was particularly evident when the female owl flew to the same mound as the male and he bent further over the lemming sheltering it from her view (Figures 10 and 11). Ritualization of basic behaviors for use in courtship is thought to have occurred in other birds (Manning, 1967).

## *Summary*

This paper reports on behavioral observations of Snowy Owls (*Nyctea scandiaca*) made on Bathurst Island, Northwest Territories during the years 1968, 1969, 1970, and 1971. I made most of the observations in 1969 when owls bred in the valley and surrounding hills between Goodsir and Bracebridge Inlets.

Snowy Owls arrive on Bathurst Island when the tundra is still snowbound. I recorded the first individual on 30 April. Courtship begins in early May. The clutch size varies from three to nine, and the female incubates for 32 to 33 days. During this time the male feeds the female.

Two displays used for courtship by male Snowy Owls are described and pictured. The aerial display consists of an undulating and jerky flight over the tundra, terminated by a gentle vertical settling to a perch. The ground display involves a stiff dance-lie posturing on hummocks, with wings partly open and raised. Both are easily visible from considerable distances. A lemming is usually carried and its importance in the evolution of the display

and as a possible adaptation for determining successful breeding in a particular year are discussed. Territorial Hooting in Snowy Owls is illustrated and described briefly.

Work on Bathurst Island is continuing. Further observations on Snowy Owls should clarify some of the points discussed.

## *Acknowledgments*

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# AVIAN EVOLUTION IN THE ARIDLANDS OF NORTH AMERICA

JOHN P. HUBBARD

Deserts, plains, and other xeric habitats dominate much of the lowlands of western North America. In spite of their harsh climates, and dearth of arboreal vegetation, such aridlands support a diverse avifauna, including many endemics and near-endemics. The North American aridlands undoubtedly date from at least the Pliocene, but their long history has not been without transformations. As recently as the last (Wisconsin) glaciation, the shift toward cooler and moister climatic conditions severely reduced the extent of these aridlands, and probably fragmented them into a series of small refugia, in which xerophilous animals — those adapted to arid conditions — survived. Such fragmentation probably took place during each of the four major glacial epochs of the Pleistocene, over a period of one to two million years. During the intervals between glaciations, the aridlands probably enjoyed a continuous distribution, much as occurs today and as probably existed during part of the Pliocene.

The changes in area of the aridlands, and other changes brought about by the alternation of glacial and interglacial intervals, doubtless affected profoundly the avifauna. The glacial intervals, with their refugial effects, probably caused the extinction of some aridlands birds, and forced other species to adapt to less xeric habitats in order to survive. Perhaps this shifting, or broadening, in adaptation is still mirrored in the avifauna, as many aridland species are markedly plastic in their selection of habitat. Another effect of the Pleistocene alterations, and the one on which I will focus attention in this paper, is that of promoting differentiation in the avifauna of the aridlands and associated areas. To account for this differentiation, I wish to propose and elaborate upon several models.

Basically, the models presented here are variations on a theme proposed by Rand (1948) and elaborated on by Mengel (1964, 1970) and others. The theme involves two steps: first, an ancestral species becomes continuously distributed over a wide area, generally in an interglacial; second, the species then is fragmented into two or more islolates by glacial events, with each isolate differentiating in turn. These models are based mainly on the study of patterns of differentiation and distribution in modern birds and paleoecological data.

I focus my analysis on what I term the Southwestern Aridlands, which consist essentially of the xeric regions of northern Mexico and the adjacent United States. I also consider areas which seem to have shared similar evolutionary histories, especially southern Mexico and southwestern California, but also the Great Basin, Great Plains, and certain other areas. I also discuss in some detail evolutionary events centering on the Great Plains, which seem to involve considerable interplay with northern regions. The temporal emphasis is on the latter half of the Pleistocene, mainly because in working backward from the Recent Epoch (the last 10,000–12,000 years), one finds that most evolutionary patterns dealt with here require only one or two glacial intervals for reconstruction. I deal with possible cases of older evolutionary history only briefly.

I used many sources of data, including the A.O.U. Check-list (1957) and "Mexican Check-list" (Friedmann *et al.*, 1950; Miller *et al.*, 1957) for modern bird distribution, Oosting (1958) and others for modern habitat distribution, and LaMotte (1952) and many others for paleobotanical information. I developed my appreciation of the paleoecological events of the Tertiary from MacGinitie (1958), obtaining more precise and detailed refinement from my analysis of many studies of paleofloras published both before and after 1958. I also visited and/or worked in many of the areas cited here, although notable exceptions include most of Baja California, the Yucatan Peninsula, and Alaska-Siberia. Finally, I benefited from contacts with many others with similar interests, and the stimulus of their works and words has been of great value to me. Together, we are groping in a still darkened milieu for answers to evolutionary problems that are both exciting and frustrating. I present this analysis, cognizant of its flaws and with the hope that it will spur efforts to reveal truths that are only glimmers now.

## *Description of the Southwestern Aridlands*

It is not my purpose to provide a detailed biogeographical or phytoecological analysis of the Southwestern Aridlands, but only to consider these aspects in broad terms. The Southwestern Aridlands, as defined here, extend mainly in the lowlands from southeastern California (Mohave Desert) to southern Texas and southward through Baja California, Sonora, the Mexican Plateau, and northern Tamaulipas (Figure 1). This region is subdivided into the Sonoran Aridlands, which extend from Arizona and Sonora westward, and the Chihuahuan Aridlands, which lie to the east and southeast. There is some justification for designating as a separate region the area of the Chihuahuan Aridlands east of the Sierra Madre Oriental, but it is not necessary for my thesis.

The approximate line separating the Sonoran from the Chihuahuan Aridlands extends from the Mogollon Plateau in southeastern Arizona and southwestern New Mexico, southward to the Sierra Madre Occidental in northeastern Sonora and northwestern Chihuahua (Figure 1). Between the two massifs is a rather narrow gap through which lowland habitats of the Sonoran and Chihuahuan Aridlands communicate, a contact further reduced, but not severed, by the intervention of several small mountain ranges. Transmontane gaps also occur in other parts of the Southwestern Aridlands, as well as between the Aridlands and other regions. These gaps, often broad, occur through the mountains extending from southeastern New Mexico to the highlands of eastern Mexico, and also through the mountains which extend the length of Baja California and into southern

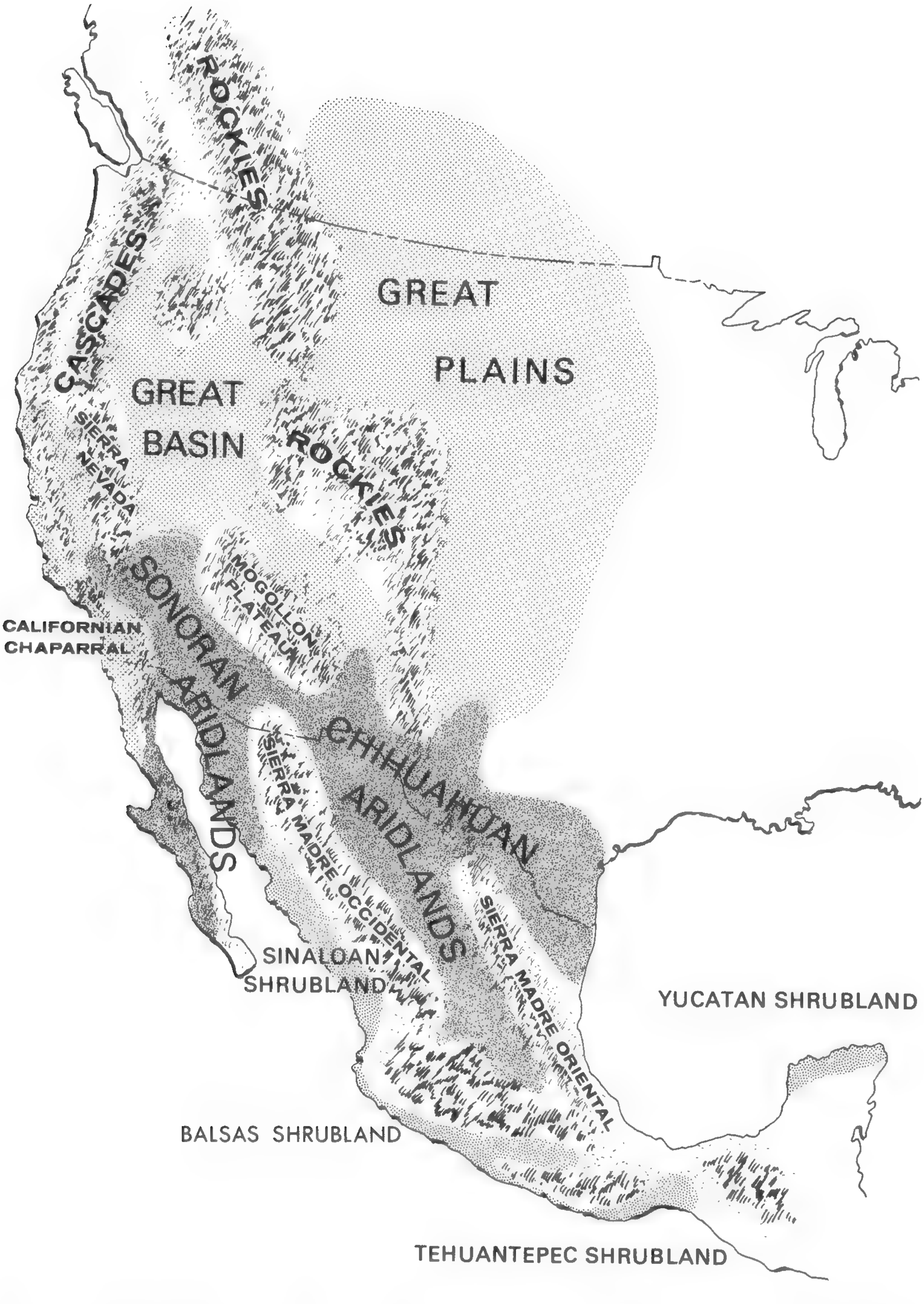
ROCKIES
GREAT
PLAINS
CASCADES
GREAT
BASIN
SIERRA
NEVADA
ROCKIES
MOGOLLON
PLATEAU
SONORAN
ARIDLANDS
CALIFORNIAN
CHAPARRAL
CHIHUAHUAN
ARIDLANDS
SIERRA
MADRE OCCIDENTAL
SIERRA
MADRE ORIENTAL
SINALOAN
SHRUBLAND
YUCATAN SHRUBLAND
BALSAS SHRUBLAND
TEHUANTEPEC SHRUBLAND

Figure 1. Major aridlands of North America, relative to highland areas. The Southwestern Aridlands are represented in two segments, the Sonoran Aridlands to the west and the Chihuahuan Aridlands to the east.

California (Figure 1). In spite of montane barriers, aridlands form an unbroken continuum across southwestern North America and also communicate with other arid and semi-arid regions of the continent. Thus, to the north, the Sonoran Aridlands merge with the Great Basin, to the south with the Sinaloan Shrubland, and to the west with the California Chaparral (or Shrubland). The Chihuahuan Aridlands merge to the north with the Great Plains and to the south with various shrubland regions. Several other xeric regions are disjunct from the Southwestern Aridlands, including especially the shrublands of Balsas Basin, the Isthmus of Tehuantepec, and the Yucatan Peninsula of Mexico (Figure 1).

Habitats over the Southwestern Aridlands vary considerably, but dominantly they consist of various types of thorny and/or succulent shrublands and xeric grasslands. Grasslands, which once characterized wide areas, especially of the western and northern Chihuahuan Aridlands, have been invaded or replaced by scrub in many places. Barren regions, such as dunes and dry lake basins, although not extensive, are widespread. Mesic habitats, such as riparian woodland and lacustrine marshes, also occur in these aridlands, although these are quite restricted in extent and have been further diminished by man's activities.

Various areas of the Southwestern Aridlands can be distinguished phytogeographically, especially on the basis of endemics. For example, *Yucca brevifolia* occurs in the Mohave Desert and vicinity, *Idria columnaris* and *Pachycormus discolor* in Baja California, and *Cereus giganteus* in Arizona and Sonora. On the other hand, several of the dominant species, such as *Larrea divaricata* and *Prosopis juliaflora,* range widely in the Southwestern Aridlands, while in other genera, such as *Acacia, Ephedra, Opuntia, Bursera, Yucca,* and *Cercidium,* closely-related replacement species grow in different areas. Thus, while botanical endemism and regional diversity exist, the similarities in dominant habitat types allow one to include this broad area of North America under the single heading of Southwestern Aridlands.

## *Pre-pleistocene History of the North American Aridlands*

The history of aridlands in North America has been pondered for some time, but in the opinion of Dr. Jerzy Rzedowski (pers. commun.), the present diversity among xerophytic plants provides perhaps the most significant clue to the age of their origin. According to him, the diversity of xerophytes, coupled with the generally slow rate of evolution in plants, indicates that they began developing in North America several million years ago and certainly well before the Pliocene. Unfortunately, there is little direct paleontological proof of such antiquity. On the other hand, a study of fossil floras from elsewhere in North America points to an increase in at least seasonal aridity through much of the Tertiary. For example, evidence of this is seen in the gradual ascendency of conifers over angiosperms in much of the western part of the continent. Even where angiosperms survived, there are such signs of adaptation to drier conditions as sclerophylly (development of certain tissues in leaves that result in thickened and hardened foliage resistant to water loss) and reduction in leaf size (e.g., in *Quercus*). Judging from these and other findings, it is likely that xerophytes almost certainly had evolved in North America by the Miocene, although perhaps only locally and mainly in the Southwest. By the middle Pliocene such habitats may have been as widespread as they are now, probably occupying such areas as the Great Basin, Great Plains, and Southwestern Aridlands.

Undoubtedly, birds inhabited these Miocene-Pliocene aridlands, but little of their nature is revealed by the meager fossil record. Precisely what one could expect, even in a more extensive record, is unclear; but it might include various raptors, gallinaceous birds, and perhaps equivalents to today's passerine seedeaters and insectivores. Whatever the exact composition of that birdlife, there is little reason to doubt the existence of a distinctively xerophilic avifauna in the aridlands of late-Tertiary North America. In fact, the remnants of that ancient avian assemblage may well persist in the present grasslands and shrublands of North America, conceivably including such genera as *Centrocercus, Geococcyx, Auriparus, Oreoscoptes, Chamaea, Dolichonyx, Spiza, Calamospiza,* and *Chondestes* — all, or most of which, appear to have no close relatives.

## *Pleistocene History of the North American Aridlands*

Regardless of what degree of diversity and distribution the North American aridlands may have achieved by the Pliocene, it seems clear that the Pleistocene Epoch and its glaciations profoundly affected that biota. Judging from events of the penultimate (Illinoian) and especially the ultimate (Wisconsin) glaciations, it seems certain that during each glacial interval the aridlands shrank drastically in size and retreated to certain refugia. The shrinkage and retreat were caused by cooler and moister conditions, which favored the spread of arboreal habitats at the expense of prairie, desert scrub, and chaparral. On the other hand, conditions during interglacials may have been at least as warm and arid as they are at present, suggesting that, during those periods, aridlands may have enjoyed a distribution similar to that of today. As already suggested, this alternate contraction and expansion of aridlands over the four glacial cycles undoubtedly had far-reaching effects, both negative and positive, on the xerophilous biota. One can visualize highly specialized aridland forms becoming extinct, because of their inability to adapt to shrunken, and probably ecologically altered, refugia. Such changes in the environment may not only have decimated the aridlands biota, but may also have forced other, more plastic, forms to adapt to altered, less xerophilous conditions. Thus, extinction and broadened adaptation may have reduced the ancient biota of the aridlands during the Pleistocene.

On the other hand, glacial fragmentation of aridlands actually may have increased the numbers of species in some groups of birds by breaking up widespread forms into isolates, each of which then may have differentiated. Such a process may have affected a substantial number of birds, although undoubtedly some species could not survive in more than one refugium. Pleistocene fragmentation and differentiation are most likely recognized by the existence of suites of closely related, often allopatric species in the North American aridlands and other regions. Members of these suites need not be restricted to aridlands, because species ranging into more mesic habitats might also have been fragmented into isolates outside the aridlands.

### Refugia for Aridland Birds during the Pleistocene

The fragmentation and differentiation among aridlands birds raises the question of where refugia may have existed during the glaciations of the

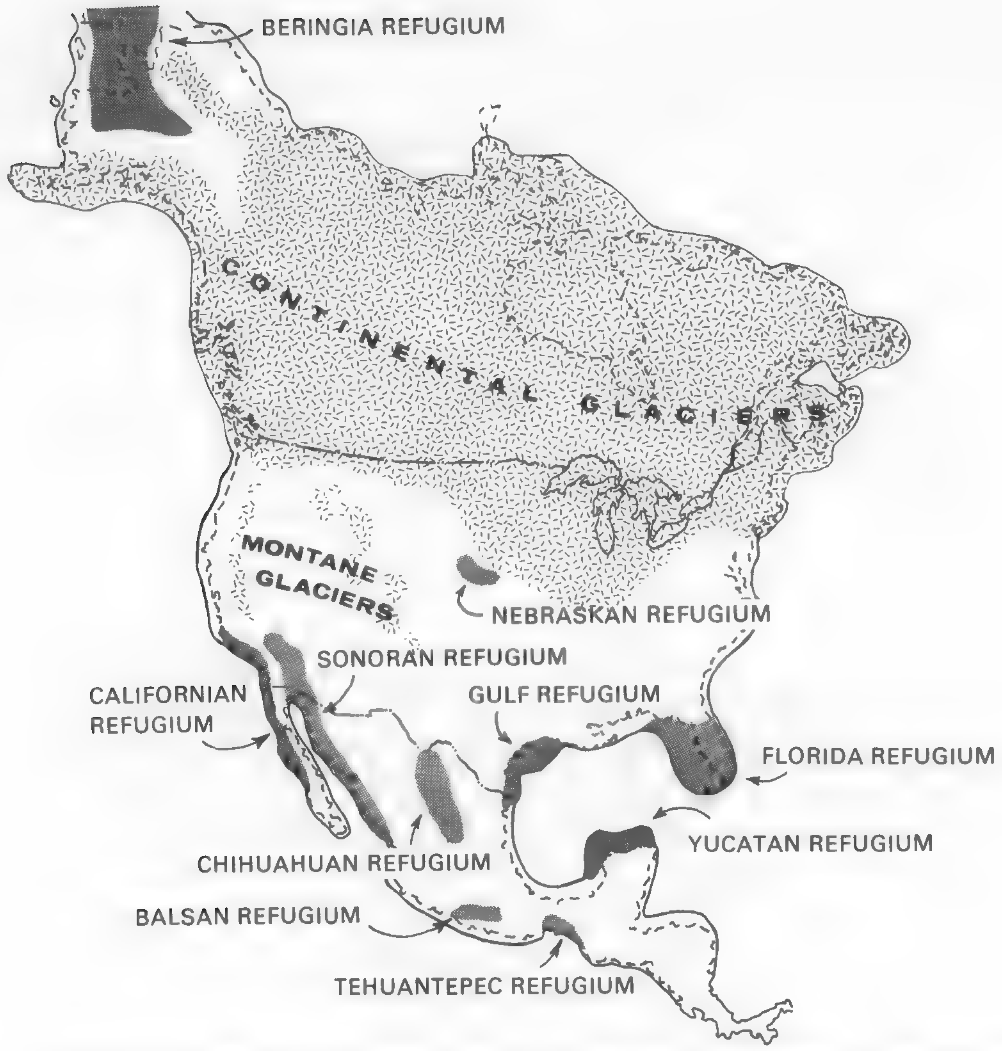
BERINGIA REFUGIUM
CONTINENTAL GLACIERS
MONTANE GLACIERS
NEBRASKAN REFUGIUM
SONORAN REFUGIUM
CALIFORNIAN REFUGIUM
GULF REFUGIUM
FLORIDA REFUGIUM
YUCATAN REFUGIUM
CHIHUAHUAN REFUGIUM
BALSAN REFUGIUM
TEHUANTEPEC REFUGIUM

Figure 2. Postulated glacial-age refugia of the aridlands and certain other regions of North America. The northern portion of the area indicated as the Sonoran Refugium probably was occupied by the biota of the Great Basin and the southern part by that of the Sinaloan Shrublands.

Pleistocene. Unfortunately, the lack of appropriate paleobotanical remains means that most of these refugia must be extrapolated on data from other sites. In spite of the speculation, the nature of the data allow at least a moderate degree of confidence in postulating the location of the refugia. In the southwestern United States, Martin and Mehringer (1965) conclude that the Wisconsin glaciation depressed the biotic zones in the Southwest by 900 to 1200 meters, indicating that woodlands and forests occurred over much of the region. They envisioned the restriction of desert scrub to extreme southwestern Arizona and southeastern California. I postulate that it extended southward into the area around the upper Gulf of California, including exposed sea bottom down to perhaps 100 meters below present sea level. This area I consider the Sonoran Refugium, supporting desert scrub and the other habitats characteristic of the region (Figure 2).

Regardless of exact location, it seems that the Sonoran Refugium was separated by a belt of forest and woodlands from the Chihuahuan Aridlands during glacial intervals. This belt extended between the Mogollon Plateau and the Sierra Madre Occidental, based on paleobotanical evidence presented by Martin (1963a). Furthermore, it seems likely that an invasion, at least of woodland, occurred over much of the Mexican Plateau (Martin, 1958), further separating and restricting aridlands. How far east and south the Chihuahuan Aridlands may have been pushed is a matter of speculation; but perhaps the most likely site for a refugium was the area west of the Sierra Madre Oriental, where a rain-shadow effect may have existed (Figure 2). The vegetation in such a refugium can be expected to have included today's Coahuilan desert scrub, plus some grassland, chaparral, and savannah. In general, the Chihuahuan Refugium was probably less favorable for desert birds than the Sonoran Refugium, but enough scrub may have existed to permit more adaptable species to persist there.

The Sonoran Refugium probably merged to the north with sagebrush and other shrubland, which would have formed the Great Basin Refugium, while to the south it may have given way to thorny woodland in the Sinaloan Refugium (Figure 2). The continuum between these three refugia contrasted with the conditions in the Chihuahuan Refugium, which was probably cut off by woodland and forest from all other aridlands.

Besides being separated from the Chihuahuan Refugium, the Great Basin-Sonoran-Sinaloan refugial areas were probably cut off from arid and semi-arid regions farther west. I postulate that on the Pacific slope there existed a Californian Refugium (Figure 2), separated by woodland and forest that extended along the Coast Range and the mountains of Baja California. The Californian Refugium may have consisted of chaparral in the north and desert scrub in the south, with part of the occupied area being exposed sea bottom.

In the Great Plains, the paleobotanical record suggests that woodland, rather than grassland, existed in most areas during glaciation. Sites studied to date include Illinoian remains from southwestern Kansas (Kapp, 1965) and Wisconsin remains from northern Nebraska (Watts and Wright, 1966) and eastern New Mexico-western Texas (Wendorf, 1961). While there is yet no evidence of the persistence of grasslands anywhere in the region during glaciation, the present prairie biota must have had such habitat to survive. A possible site for such survival, and postulated here, was the Nebraskan Sandhills region, where conditions may have been too unstable and harsh for forest until late in the Pleistocene (Wright, 1970). The Nebraskan Refugium probably merged to the north with tundra, as the periglacial boundary was not far away. Another refugium for prairie elements also may have existed farther south, probably along the Gulf of Mexico. The Gulf Refugium (Figure 2) would have consisted mainly of exposed sea bottom with sandy and saline soils that may have been edaphically, if not climatically, arid. Elements of the prairie and other aridlands could have retreated to the Gulf Refugium through southern Texas, which communicates both with the southern Great Plains and with more xeric regions to the west. While paleobotanical evidence of the Gulf Refugium is lacking, relicts of the aridlands biota in southeastern Texas-southwestern Louisiana may reflect its former existence. It is also possible that some Great Plains elements retreated to, and survived in, the Chihuahuan Refugium.

Several other refugia for aridlands or semi-aridlands elements may have existed elsewhere in North America, including Mexico and Alaska. In Mexico, montane habitats expanded into lower elevations during glacials nearly as extensively as in the southwestern United States. The influx of montane elements from the Plateau and elsewhere probably overran considerable areas of the thorn scrub and other xeric habitats of the Pacific

## TABLE 1

Endemic and Near-endemic Bird Species of the Aridlands and Adjacent Regions of North America, Showing the Major Breeding Areas and the Possible Areas of Differentiation (capitalized regions)

*Aechmophorus occidentalis* (Western Grebe)*, Great Basin, Great Plains

*Pelecanus erythrorhynchus* (White Pelican)*, Great Basin, Great Plains

*Anas [platyrhynchos] diazi* (Mexican Duck), CHIHUAHUAN ARIDLANDS

*Falco mexicanus* (Prairie Falcon)*, Sonoran Aridlands, Chihuahuan Aridlands, Great Basin, GREAT PLAINS

*Centrocercus urophasianus* (Sage Grouse), GREAT BASIN (?), Great Plains

*Callipepla squamata* (Scaled Quail), CHIHUAHUAN ARIDLANDS, Great Plains

*Callipepla [Lophortyx] gambelii* (Gambel's Quail), SONORAN ARIDLANDS, Chihuahuan Aridlands

*Charadrius [Eupoda] montanus* (Mountain Plover), Chihuahuan Aridlands, Great Basin, GREAT PLAINS (?)

*Numenius americanus* (Long-billed Curlew), Great Basin, GREAT PLAINS

*Limosa fedoa* (Marbled Godwit), Great Basin, GREAT PLAINS

*Phalaropus [Steganopus] tricolor* (Wilson's Phalarope)*, Great Basin, GREAT PLAINS

*Larus pipixcan* (Franklin's Gull), Great Basin, Great Plains

*Geococcyx californianus* (Roadrunner)*, SONORAN ARIDLANDS, Chihuahuan Aridlands, Great Basin, Great Plains

*Archilochus [Calyptes] costae* (Costa's Hummingbird)*, SONORAN ARIDLANDS

*Colaptes [auratus] chrysoides* (Gilded Flicker)*, SONORAN ARIDLANDS

*Tyrannus [Muscivora] forficatus* (Scissor-tailed Flycatcher)*, GREAT PLAINS

*Corvus cryptoleucus* (White-necked Raven)*, Chihuahuan Aridlands, GREAT PLAINS (?)

*Auriparus flaviceps* (Verdin)*, Sonoran Aridlands, Chihuahuan Aridlands

*Campylorhynchus brunneicapillus* (Cactus Wren)*, SONORAN ARIDLANDS, Chihuahuan Aridlands, Great Plains

*Oreoscoptes montanus* (Sage Thrasher), GREAT BASIN (?), Great Plains

*Toxostoma bendirei* (Bendire's Thrasher), SONORAN ARIDLANDS, Chihuahuan Aridlands

*Toxostoma cinereum* (Gray Thrasher), SONORAN ARIDLANDS

*Toxostoma dorsale* (Crissal Thrasher), Sonoran Aridlands, CHIHUAHUAN ARIDLANDS

*Toxostoma lecontei* (Leconte's Thrasher)*, SONORAN ARIDLANDS

*Polioptila melanura* (Black-tailed Gnatcatcher)*, SONORAN ARIDLANDS, Chihuahuan Aridlands

*Anthus spragueii* (Sprague's Pipit), GREAT PLAINS

*Vireo atricapilla* (Black-capped Vireo)*, GREAT PLAINS

*Vireo bellii* (Bell's Vireo)*, Sonoran Aridlands, Chihuahuan Aridlands, Great Plains

*Vermivora luciae* (Lucy's Warbler), SONORAN ARIDLANDS, Chihuahuan Aridlands

*Xanthocephalus xanthocephalus* (Yellow-headed Blackbird)*, Sonoran Aridlands, Chihuahuan Aridlands, Great Basin, Great Plains

TABLE 1 (*Continued*)

*Cardinalis* [*Pyrrhuloxia*] *sinuatus* (Pyrrhuloxia)*, SONORAN ARIDLANDS (?), Chihuahuan Aridlands, Great Plains

*Pipilo aberti* (Abert's Towhee), SONORAN ARIDLANDS

*Pipilo fuscus* (Brown Towhee)*, Sonoran Aridlands, CHIHUAHUAN ARIDLANDS, Great Plains

*Calamospiza melanocorys* (Lark Bunting), GREAT PLAINS (?)

*Amphispiza bilineata* (Black-throated Sparrow)*, SONORAN ARIDLANDS, Chihuahuan Aridlands, Great Basin, Great Plains

*Amphispiza belli* (Sage Sparrow)*, Great Basin

*Aimophila cassinii* (Cassin's Sparrow), CHIHUAHUAN ARIDLANDS, Great Plains

*Spizella wortheni* (Worthen's Sparrow), CHIHUAHUAN ARIDLANDS

*Spizella pallida* (Clay-colored Sparrow)*, GREAT PLAINS

*Spizella breweri* (Brewer's Sparrow)*, GREAT BASIN, Great Plains

*Calcarius ornatus* (Chestnut-collared Longspur), GREAT PLAINS

*Calcarius* [*Rhynchophanes*] *mccownii* (McCown's Longspur), GREAT PLAINS

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*Indicates a form that also breeds outside of aridlands.

slope. The xerophytic continuum that presently exists between Sonora and Chiapas probably broke at several points, resulting in the formation of refugia in enclaves in the Balsas Basin, southernmost Isthmus of Tehuantepec, and the aforementioned Sinaloan region (Figure 2). In addition, another xeric refugium probably formed in the tip of the Yucatan Peninsula, and possibly others farther south in Central America. Connections between arid habitats of the Yucatan Peninsula and those of the Pacific Slope may have occurred only during the most xeric phases of the interglacials. Otherwise, these areas probably remained separated by mesic habitats during most of the interglacials, as they are now.

In Alaska, the existence of a refugium is indicated by paleontological evidence, and the Alaskan Refugium was actually part of a larger area called Beringia (Figure 2), which included eastern Siberia and the exposed Bering Strait (Hopkins, 1967). Association of that northern region with aridlands farther south is based on a number of factors, including present ecological and biogeographical relationships. Furthermore, during the Wisconsin, much of Beringia seems to have been grassland, thus allying it ecologically with the more southern prairies of North America.

## Recent Changes in the Aridlands Refugia

The period of 10,000 to 15,000 years that has elapsed since the close of the last glaciation is generally called the Recent Epoch, although by many it is regarded as an extension of the Pleistocene. In the early Recent, xeric habitats of North America spread from their glacial-age refugia as conditions became warmer and more arid. Eventually, aridlands reclaimed all of the region they now occupy. In fact, from about 9,000 to 2,500 years ago, xeric habitats may have been even more extensive than now. That span of time is referred to as the Altithermal Interval (Deevy and Flint, 1957). During that period, it seems likely that xeric habitats invaded several presently mesic regions, allowing the spread of various xerophilic organisms, including birds. For example, the Great Plains biota may have penetrated into the Great Lakes region at that time, thus accounting for prairie elements there. Other xeric corridors may have extended between the Isthmus of Tehuantepec to Yucatan, and between the Mohave Desert and the San Joaquin Valley of California. The expansion of aridlands during the Altithermal may not have been universal in North America, e.g., in Arizona (Martin, 1963b), but it seems to have been a widespread phenomenon. Additional expansions of aridlands may have occurred at other times during the Recent Epoch, possibly early in the period, but expansion during the Altithermal seems to have been the most significant.

Summarizing, the Southwestern Aridlands doubtlessly retreated and became fragmented during the Pleistocene glaciations, and expanded to become continuous during interglacials, as they are today and probably were during the middle Pliocene. During glaciation these aridlands probably survived in refugia in the eastern Mexican Plateau (the Chihuahuan Refugium) and in the upper Gulf of California area (the Sonoran Refugium). The latter was probably continuous with the Great Basin and Sinaloan refugia, while the Chihuahuan Refugium may have been separated from all other aridlands. Other important refugia of glacial age may have been on the Pacific slope of the Californias, in the Nebraskan Sandhills, on the upper Gulf of Mexico, in Beringia, and in Mexico in the Balsas, Tehuantepec, and Yucatan regions. Following the end of the last glaciation, aridlands expanded and, in the Altithermal Interval, may have been more extensive than they are now.

## *Composition of the Avifauna of the North American Aridlands and Associated Areas*

In Table 1, I have listed and tabulated what I consider to be essential avifaunal elements of the aridlands of North America. This list contains the endemics of the Southwestern Aridlands, Great Basin, Great Plains, and associated areas. I also included most of the species having ranges largely confined to these aridlands, but which range in varying degrees into other areas. The decision to include or exclude various species in the second category is arbitrary, but I have tried to include those species that range only narrowly outside the aridlands in North America. I have excluded more wide-ranging species, such as many waterbirds, Swainson's Hawk (*Buteo swainsoni*), Prairie Grouse (*Tympanuchus cupido*), Ladder-backed Woodpecker (*Dendrocopos scalaris*), Western Kingbird (*Tyrannus verticalis*), Rock Wren (*Salpinctes obsoletus*), Western Meadowlark (*Sturnella neglecta*), and House Finch (*Carpodacus mexicanus*). I have included several aridlands forms that may not be full species (here called semi-species), but have eliminated others that clearly seem to be subspecies of wider-ranging species, such as the Willet (*Catoptrophorus semipalmatus inornatus*), Burrowing Owl (*Speotyto cunicularia hypugaea*), and Summer Tanager (*Piranga rubra cooperi*). For other concepts of the North American aridlands avifauna, see papers by Udvardy (1958) and Mengel (1970).

At this point I will reconstruct the possible evolutionary histories of certain species and semi-species, with emphasis on those and their relatives in Table 1, but also including others not listed. Not all of the listed species invite analysis, for reasons which include their apparent lack of near relatives, suggesting a less recent origin, and/or their peculiarities in ranges,

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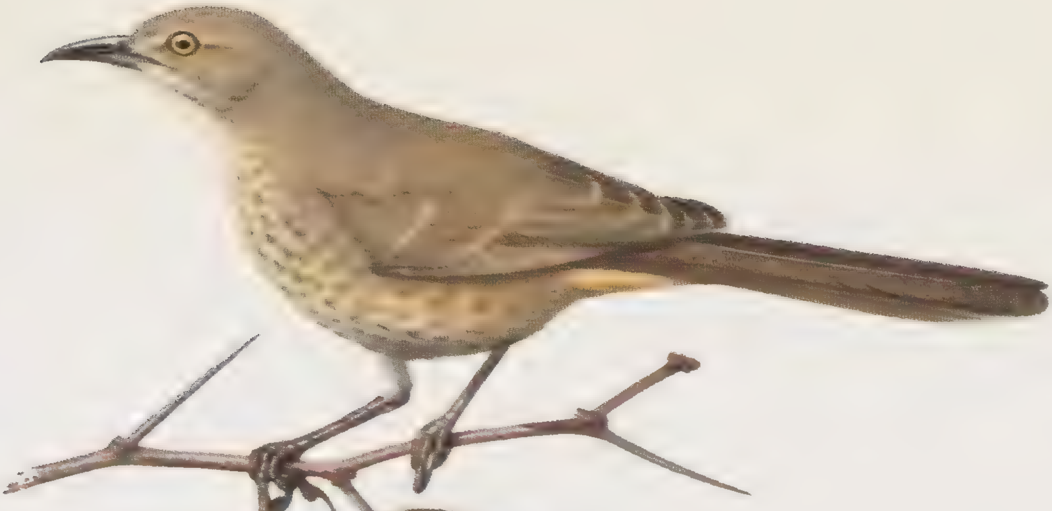
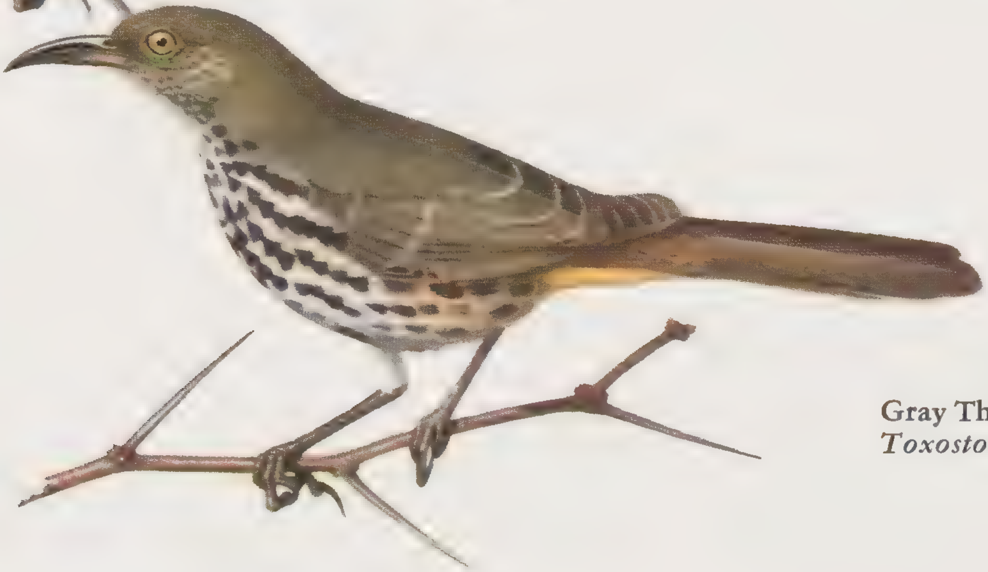
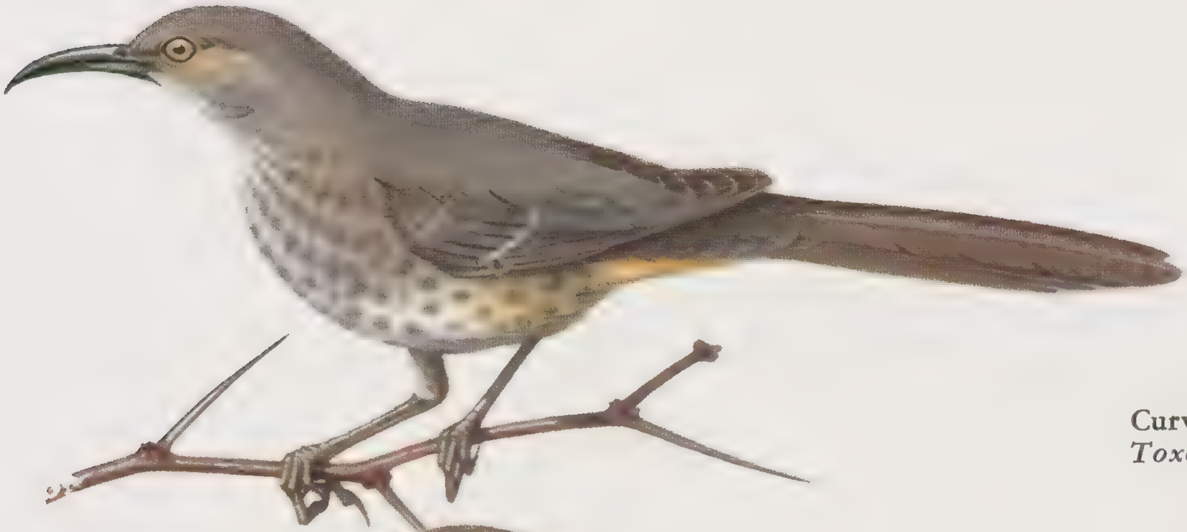
**Curve-billed Thrasher complex. Painting by Orville O. Rice.**



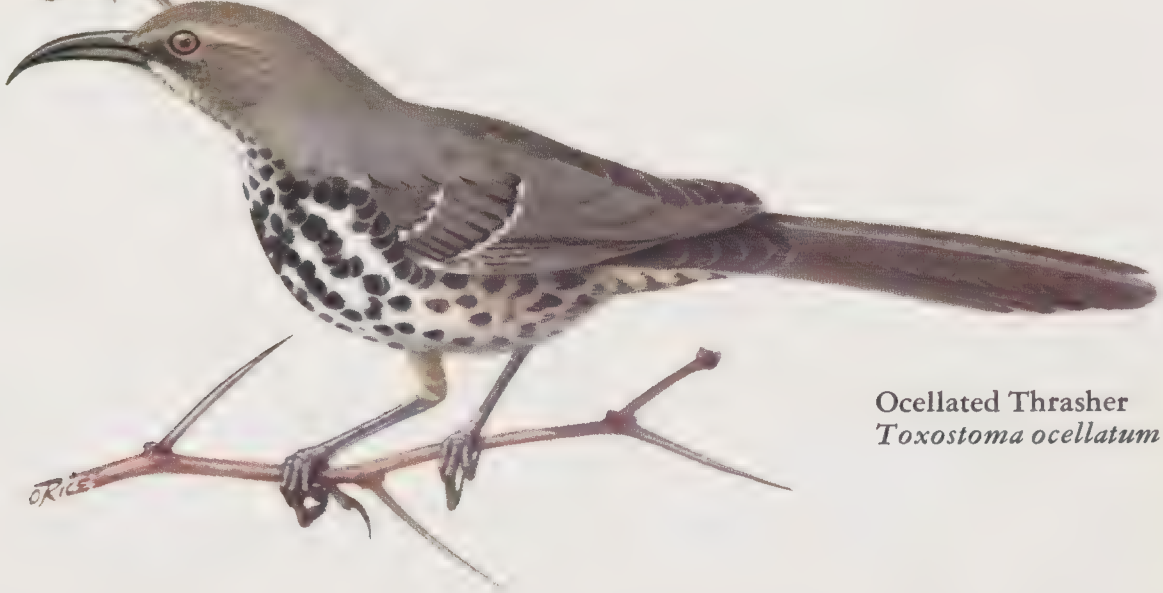
Bendire's Thrasher
*Toxostoma bendirei*



Gray Thrasher
*Toxostoma cinereum*



Curve-billed Thrasher
*Toxostoma curvirostre*



Ocellated Thrasher
*Toxostoma ocellatum*

which might obscure their origin. Species not investigated for these reasons include the Western Grebe (*Aechmophorus occidentalis*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and certain others on Page 000, which may represent remnants of the theoretical avifauna of the Mio-Pliocene aridlands of North America. A number of other species such as the White Pelican (*Pelecanus erythrorhynchus*) and Franklin's Gull (*Larus pipixcan*),have congeneric relatives still extant; but because of distributional anomalies or other factors, I will not probe their possible evolutionary histories here.

Many of the remaining species of the aridlands avifauna of North America at least yield glimmers of their possible evolutionary histories, which appear to involve variations on the previously mentioned Pleistocene evolutionary model. As I have already indicated, the model first assumes that an ancestral form achieved a wide range during an interglacial, and was secondarily fragmented and isolated in at least two refugia during the succeeding glacial advance. While isolated in these refugia, differentiation occurred, ultimately leading to speciation. This cycle may have been repeated, as one or more of the differentiates spread during a subsequent interglacial, only to become fragmented, and possibly differentiated, in the next glacial interval.

All of the refugia of the aridlands appeared to have been involved in the speciation of birds during the Pleistocene, but not to the same degree. The Sonoran and Chihuahuan refugia appear to have interacted with each other as well as with the Californian and Balsan refugia. However, relatively less interplay is indicated with the Great Basin and Great Plains, which, in turn, were largely independent of each other. In the differentiation of populations in the Great Plains, the interacting partner often was to the north, in Beringia and perhaps Eurasia, although some degree of interplay is indicated with more southern areas. The Great Basin hosts few endemics, or species that seem to have originated there, these including such seemingly older (pre-Pleistocene?) forms as the Sage Grouse (*Centrocercus urophasianus*), and Sage Thrasher (*Oreoscoptes montanus*), whose origins are obscure.

## *Pleistocene Differentiation of the Avifauna*

As mentioned above, avian evolution in the Southwestern Aridlands during the Pleistocene seems largely to have involved a concert of interaction between the Sonoran, Chihuahuan, Californian, and Balsan Refugia. Several modern species groups seem to have arisen from this interaction. Before discussing them, however, I wish to demonstrate the workings of the model with a single modern species, the Cactus Wren (*Campylorhynchus brunneicapillus*). This species occurs widely in the Southwestern Aridlands and also extends to the southernmost Great Basin and Great Plains, southwestern California, and northern Sinaloa (Figure 3). If glacial conditions returned to North America, this wide-ranging and continuously distributed species could be fragmented into several populations, conceivably in the Californian, Sonoran, and Chihuahuan refugia. In those refugia, the three isolates could diverge and differentiate. Thus, what began as one species might become three, as the result of a fragmentation of aridlands during a glacial interval. If additional isolates survived in other areas, such as the

Balsan and Gulf refugia, an even greater proliferation of species could occur. In fact, *C. brunneicapillus* may result from the fragmentation of a scrub-loving ancestor which arose during glacial isolation, perhaps in the Sonoran Refugium, while to the south the related Spotted Wren (*C. jocosus*) may have differentiated simultaneously (Selander, 1964), perhaps in the Balsan Refugium, and yet another near relative (*C. yucatanicus*), differentiated during the same period in the Yucatan Peninsula. Thus, one can see from this example how species might arise and proliferate from a single ancestor in the Southwestern Aridlands and associated areas. Four species complexes invite detailed examination in light of this model (in order of increasing complexity): the Crissal Thrasher complex, the Curve-billed Thrasher complex, the Brown Towhee complex, and the Scaled Quail complex (Table 2).

## Crissal Thrasher Complex

This consists of the Crissal (*Toxostoma dorsale*), LeConte's (*T. lecontei*), and California (*T. redivivum*) Thrashers, all of which appear closely related (Engels, 1940). *T. lecontei* is sympatric with the other two (which are allopatric to each other), although ecologically, it is generally separate from them (Figure 4). This complex appears to have a relatively simple history, probably resulting from a single fragmentation of a wide-ranging ancestral form into three refugial isolates: Californian (pre-*redivivum*), Sonoran (pre-*lecontei*), and Chihuahuan (pre-*dorsale*) (Figure 5). Following their differentiation, these species spread as their habitats expanded, subsequently developing sympatry. Thus, *dorsale* spread westward into the Sonoran Aridlands, while *lecontei* spread westward into Baja California and the arid San Joaquin Valley area of California. *Redivivum* remains west and north of the desert areas of the Sonoran Aridlands, perhaps because of competition with *dorsale*. The latter seems ecologically more similar to it than *lecontei*. Differentiation of this complex may have originated with the Wisconsin glaciation, with range expansion and sympatry being achieved in the Recent Period.

## Curve-billed Thrasher Complex

This complex consists of the Curve-billed (*T. curvirostre*), Bendire's (*T. bendirei*), Gray (*T. cinereum*), and Ocellated (*T. ocellatum*) Thrashers, closely related among themselves, but perhaps not to the same degree as the members of the Crissal Thrasher complex (Engels, 1940). Within this complex there are two species pairs, namely, *bendirei-cinereum*, which are allopatric, and *curvirostre-ocellatum*, which are sympatric; *bendirei* and *curvirostre* are also sympatric (Figure 6). Quite likely, these species originated in the following refugia: Californian (pre-*cinereum*), Sonoran (pre-*bendirei*), Chihuahuan (pre-*curvirostre*), and Balsan (pre-*ocellatum*). The question is, how many disjunctions were involved to produce this complex? One theory is that a single wide-ranging ancestor may have fragmented into the precursor populations in the above four refugia. More likely, however, the species arose from multiple disjunctions involving two glacials (Figure 7). During the first glacial, a single ancestral species may have separated into two populations — pre-*bendirei/cinereum* in the west, probably in the Sonoran Refugium, and pre-*curvirostre/ocellatum* in the east, probably in the Chihuahuan Refugium. After these two isolates diverged to the species

## TABLE 2

## Probable Differentiates of the Sonoran, Chihuahuan, and Associated Glacial Age Refugia of the Pleistocene Epoch

| *Probable differentiates of the Sonoran Refugium* | *Probable differentiates of the Chihuahuan Refugium* | *Certain related forms and probable areas of differentiation* |
|---|---|---|
| | *Anas [platyrhynchos] diazi* (Mexican Duck) | *Anas platyrhynchos* (Mallard), Palearctic<br>*A. rubripes* (Black Duck), Eastern North America<br>*A. [p.] fulvigula* (Mottled Duck), Gulf Refugium |
| *Callipepla [Lophortyx] gambelii* (Gambel's Quail)<br>*C. [L.] douglasii* (Elegant Quail) | *C. squamata* (Scaled Quail) | *Callipepla [L.] californica* (California Quail), California Refugium |
| *Archilochus [Calypte] costae* (Costa's Hummingbird) | | *Archilochus colibri* (Ruby-throated Hummingbird), Eastern North America<br>*A. alexandri* (Black-chinned Hummingbird), Western North America<br>*A. [C.] anna* (Anna's Hummingbird), Californian Refugium |
| *Colaptes [auratus] chrysoides* (Gilded Flicker) | | *Colaptes auratus* (Yellow-shafted Flicker), Eastern North America<br>*C. [a.] cafer* (Red-shafted Flicker), Western North America |
| *Toxostoma bendirei* (Bendire's Thrasher) | *T. curvirostre* (Curve-billed Thrasher) | *Toxostoma cinereum* (Gray Thrasher), Californian Refugium<br>*T. ocellatum* (Ocellated Thrasher), Balsan Refugium |
| *Toxostoma lecontei* (Leconte's Thrasher) | *T. dorsale* (Crissal Thrasher) | *T. redivivum* (California Thrasher), Californian Refugium |
| *Vermivora luciae* (Lucy's Warbler) | *V. virginiae* (Virginia's Warbler)<br>*V. crissalis* (Colima Warbler) | *Vermivora ruficapilla* (Nashville Warbler), Californian Refugium |
| *Pipilo aberti* (Abert's Towhee) | *P. fuscus* (Brown Towhee) | *Pipilo [f.] crissalis* (Brown Towhee), Californian Refugium<br>*P. albicollis* (White-throated Towhee), Balsan Refugium |
| | *Aimophila cassinii* (Cassin's Sparrow) | *Aimophila aestivalis* (Bachman's Sparrow), Florida Refugium<br>*A. botterii* (Botteri's Sparrow), Tehuantepec Refugium<br>*A. petenica* (Yellow-carpalled Sparrow), Yucatan(?) Refugium |
| | *Spizella wortheni* (Worthen's Sparrow) | *S. pusilla* (Field Sparrow), Florida Refugium |

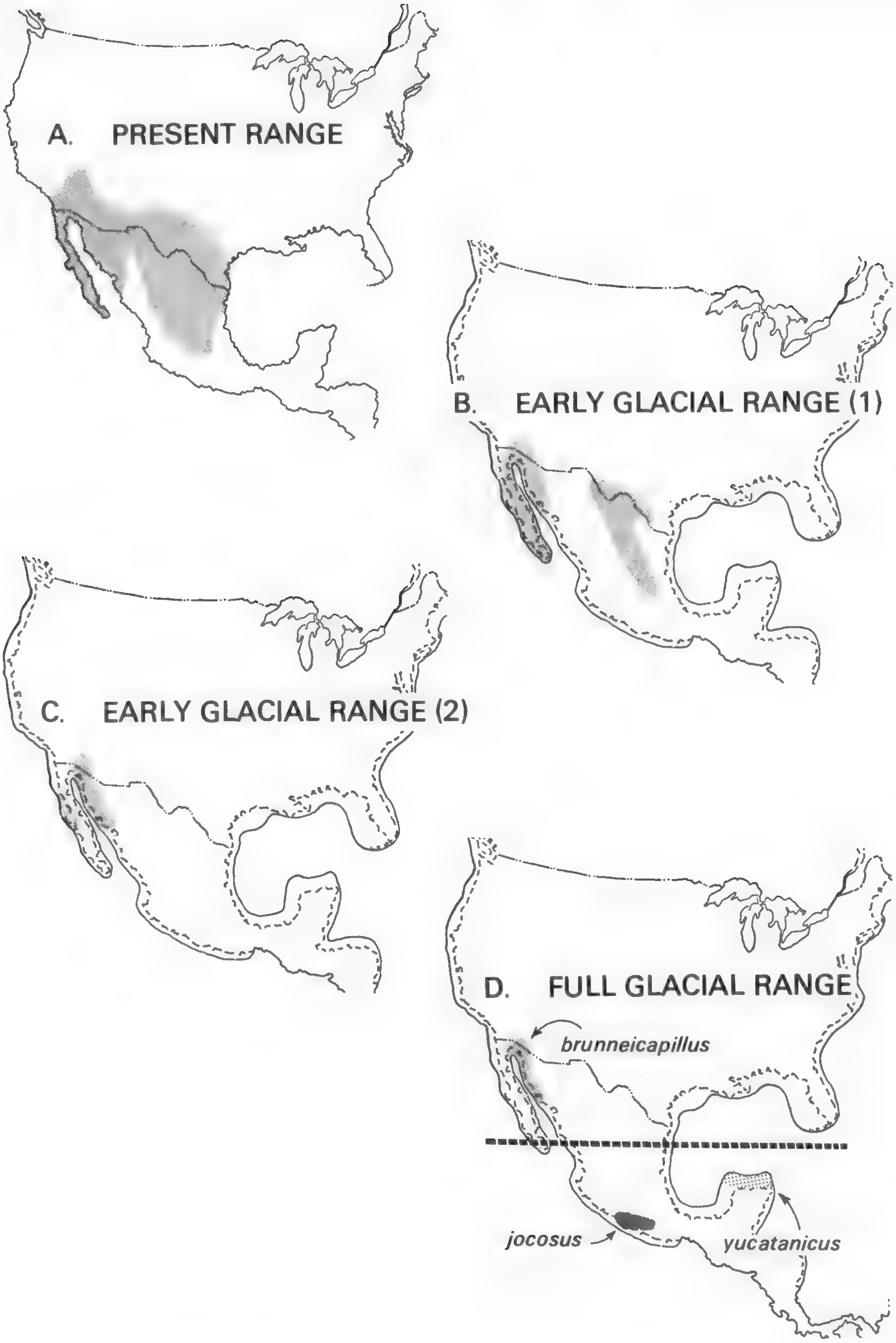

A. PRESENT RANGE
B. EARLY GLACIAL RANGE (1)
C. EARLY GLACIAL RANGE (2)
D. FULL GLACIAL RANGE
brunneicapillus
jocosus
yucatanicus

Figure 3. Postulated alteration in the range (A) of the Cactus Wren (*Campylorhynchus brunneicapillus*) that might occur in the face of a future glacial cycle (B and C), and possible areas of origin of this species and two relatives, *C. jocosus* and *C. yucatanicus* during a past glaciation (D).

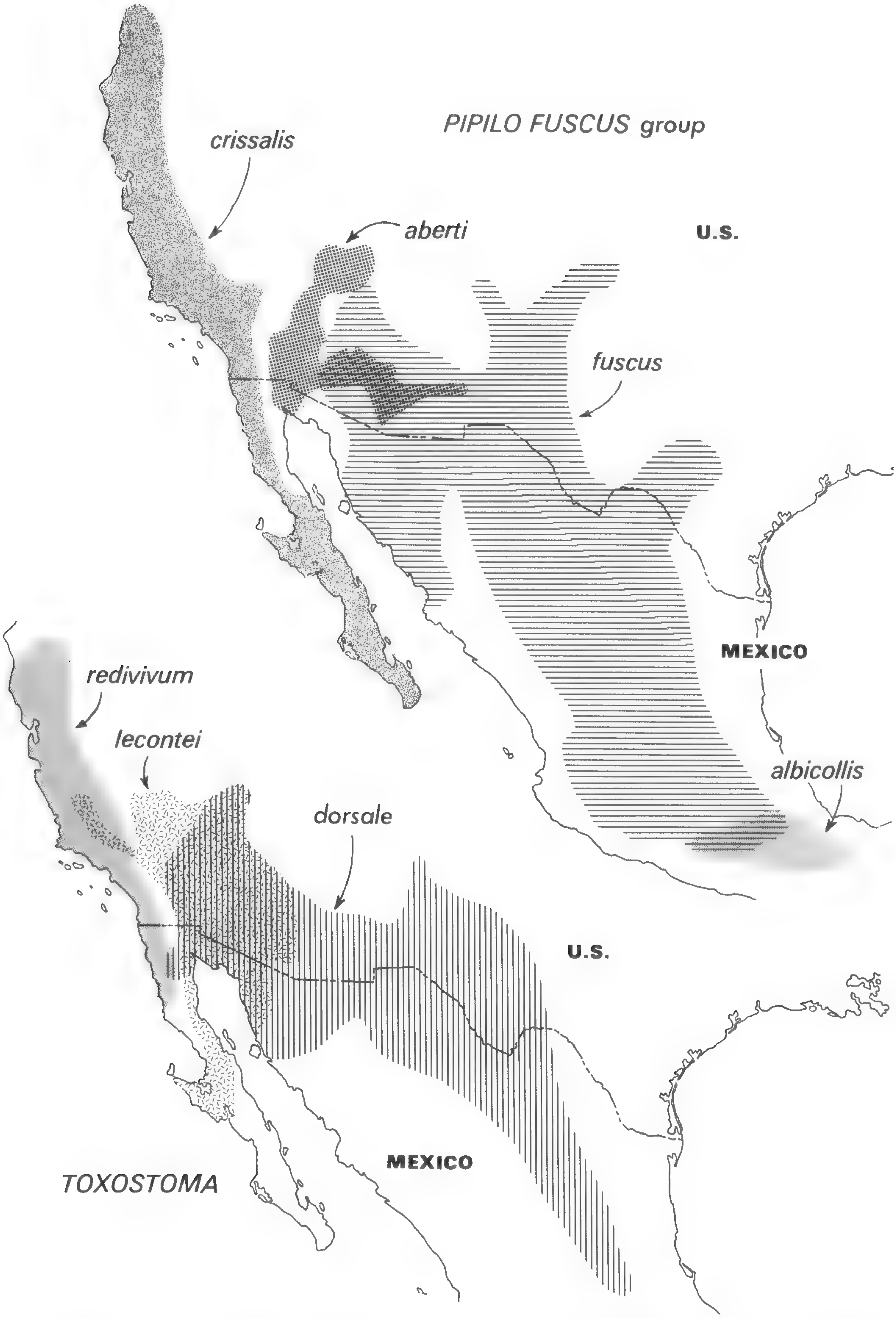
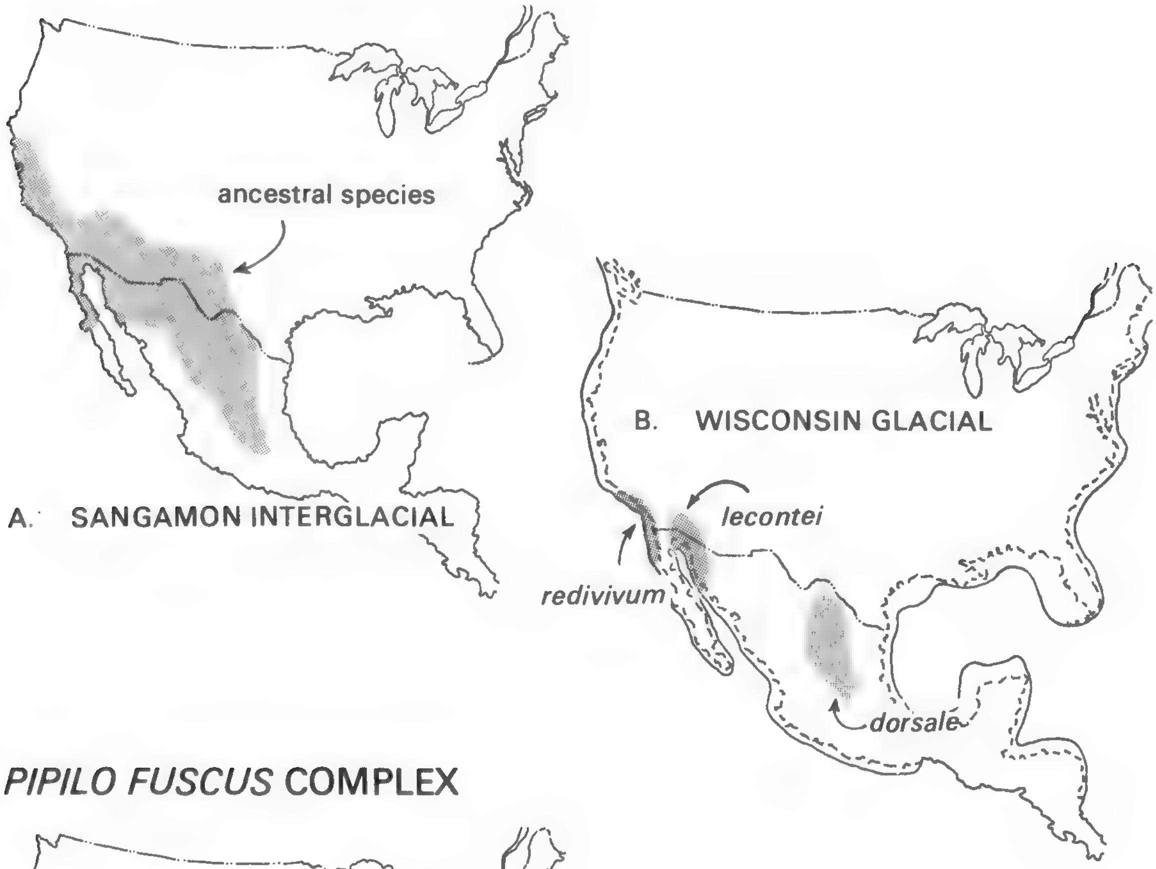

PIPILO FUSCUS group
crissalis
aberti
U.S.
fuscus
MEXICO
albicollis
redivivum
lecontei
dorsale
U.S.
MEXICO
TOXOSTOMA

Figure 4. *Upper,* modern range of the Brown Towhee complex (*Pipilo fuscus* and its relatives). *Lower,* modern range of the Crissal Thrasher complex (*Toxostoma dorsale*) and its relatives.

*TOXOSTOMA DORSALE* COMPLEX


ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
lecontei
redivivum
dorsale

*PIPILO FUSCUS* COMPLEX

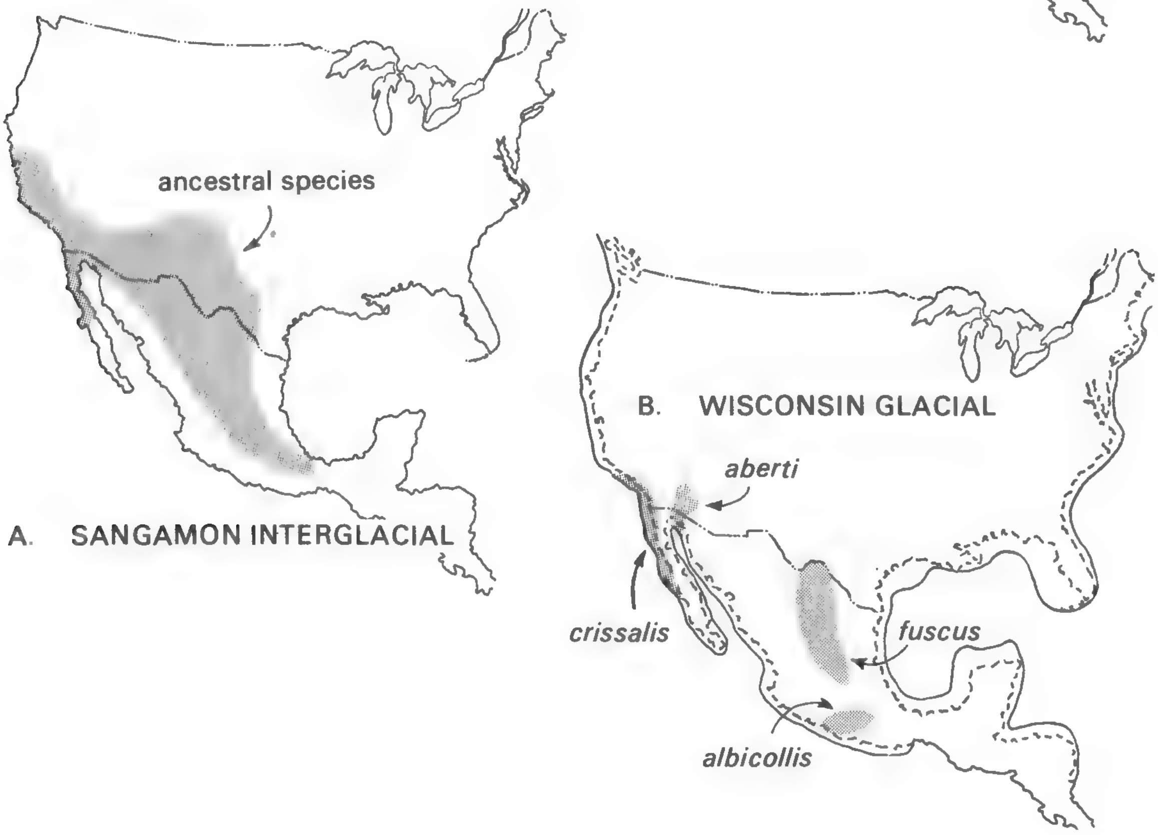

ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
aberti
crissalis
fuscus
albicollis

Figure 5. *A*, possible mode of differentiation of the Crissal Thrasher (*Toxostoma dorsale*) complex, showing postulated refugial origins. *B*, possible mode (simple version) of differentiation of the Brown Towhee (*Pipilo fuscus*) complex, showing postulated refugial origins.

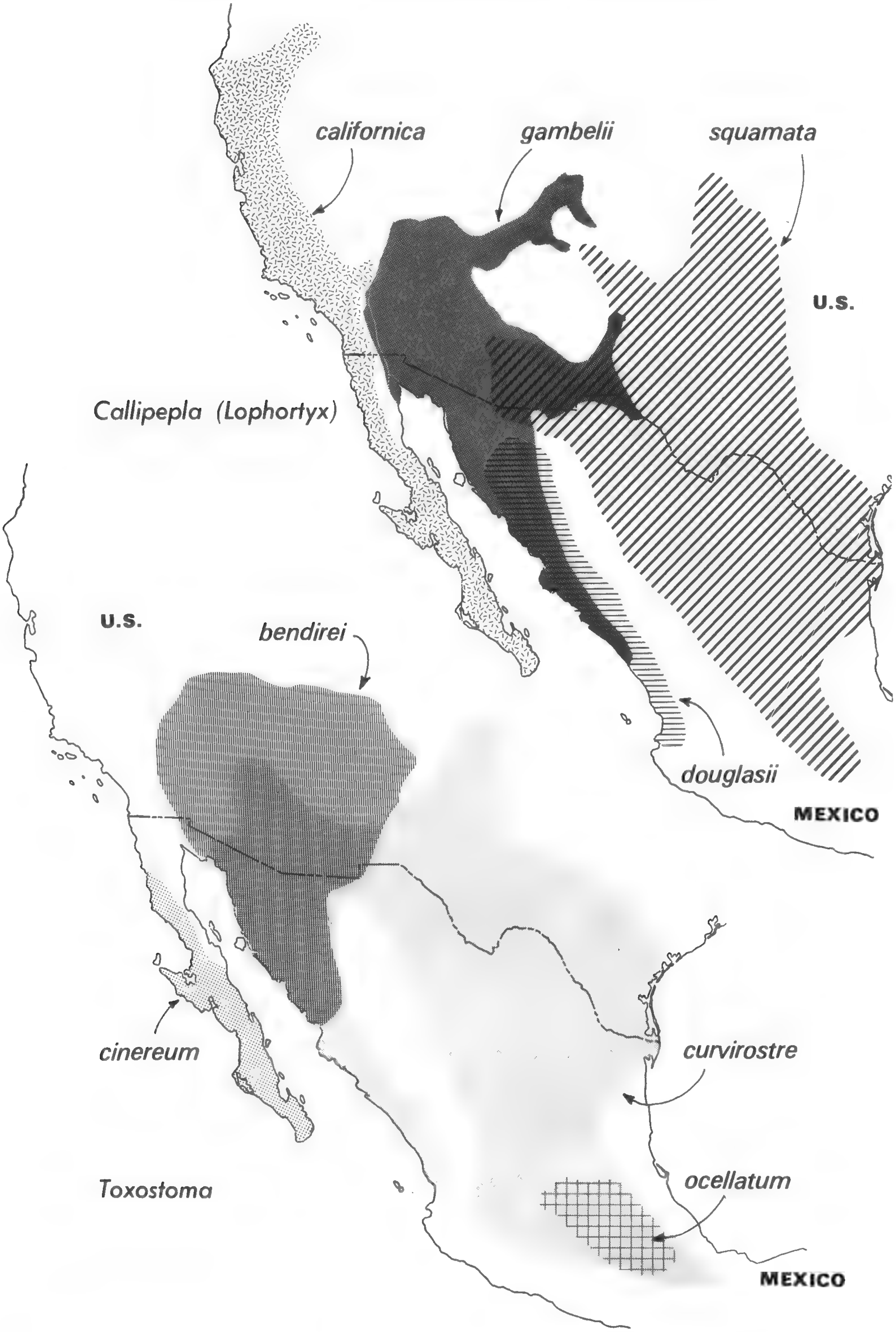

californica
gambelii
squamata
U.S.
Callipepla (Lophortyx)
douglasii
MEXICO
U.S.
bendirei
cinereum
curvirostre
ocellatum
Toxostoma
MEXICO

Figure 6. *Upper,* modern range of the Scaled Quail complex (*Callipepla squamata* and its relatives). *Lower,* modern range of the Curve-billed Thrasher complex (*Toxostoma curvirostre* and its relatives).

level and the glacial recession occurred, pre-*bendirei/cinereum* may have spread westward into Baja California, while pre-*curvirostre/ocellatum* spread southward to the Balsas region. With the next glaciation, the precursors of the four modern species may then have become isolated into the four refugia outlined above. Following differentiation and deglaciation, *curvirostre* may have expanded westward into the Sonoran Aridlands to become sympatric with *bendirei.* The latter also invaded the Chihuahuan Aridlands to a lesser degree. The marked geographic variation in *curvirostre* probably arose during the Recent Epoch. Thus, the two species groups in the Curve-billed Thrasher complex could have differentiated as long ago as the Illinoian glaciation, with modern species dating from the Wisconsin glaciation.

Related to the Curve-billed Thrasher complex is the Brown Thrasher complex, consisting of the Brown (*Toxostoma rufum*), Long-billed (*T. longirostris*), and Cozumel (*T. guttatum*) Thrashers (Engels, 1940). These species are allopatric, with *rufum* in the United States, *longirostris* in eastern Mexico, and *guttatum* on Cozumel Island off the Yucatan Peninsula. The Brown Thrasher complex is perhaps a little more distantly related to *curvirostre-ocellatum* than is *bendirei-cinereum,* but the three groups seem to form a closely-knit unit. The Brown Thrasher complex may have split off at about the same time as the Curve-billed Thrasher complex split into its two main components. After the split occurred, the precursor of the Brown Thrasher group probably achieved a continuous distribution from the eastern United States to the Yucatan Peninsula and vicinity, only to be fragmented, probably during the Wisconsin, into the three isolates that gave rise to the modern species as in their present ranges.

## Brown Towhee Complex

This complex consists of the Brown (*Pipilo fuscus*), Abert's (*P. aberti*), and White-throated (*P. albicollis*) Towhees, the first of which is divisible into two main groups: the *crissalis* group of the Pacific Coast and the *fuscus* group of Mexico and the Southwest (Figure 4). The allopatric *crissalis* and *fuscus* groups have been regarded as different species, as they differ in morphology, voice, and other characteristics (Davis, 1951; Marshall, 1964). However, in southern Baja California the race *albigula* is very similar in color and pattern to the *fuscus* group, which has led to merging of the two groups, although they differ in voice and egg color. *Aberti* is in some ways similar in voice to *crissalis,* while *fuscus* and *albicollis* are even more similar in this respect to each other (Marshall, 1964).

Davis (1951) speculated in a general way on the evolution of this complex of towhees, but he based his now-outdated model on an unrefined Pliocene picture. In my opinion, the members of the complex are of Pleistocene age, and could have arisen as recently as the Wisconsin through a single cycle of glacial-age isolation (Figure 5). The refugial origins seem clearly demarked, i.e., Californian (pre-*crissalis*), Sonoran (pre-*aberti*), Chihuahuan (pre-*fuscus*), and Balsan (pre-*albicollis*). With deglaciation, the range of *fuscus* could have expanded westward into the Sonoran Aridlands and southward into southern Mexico, thus producing overlap with *aberti* and *albicollis,* respectively (Figure 4). Actually, the picture may be more complicated than this, and the development of an alternative model seems worthwhile.

## *TOXOSTOMA CURVIROSTRE* COMPLEX

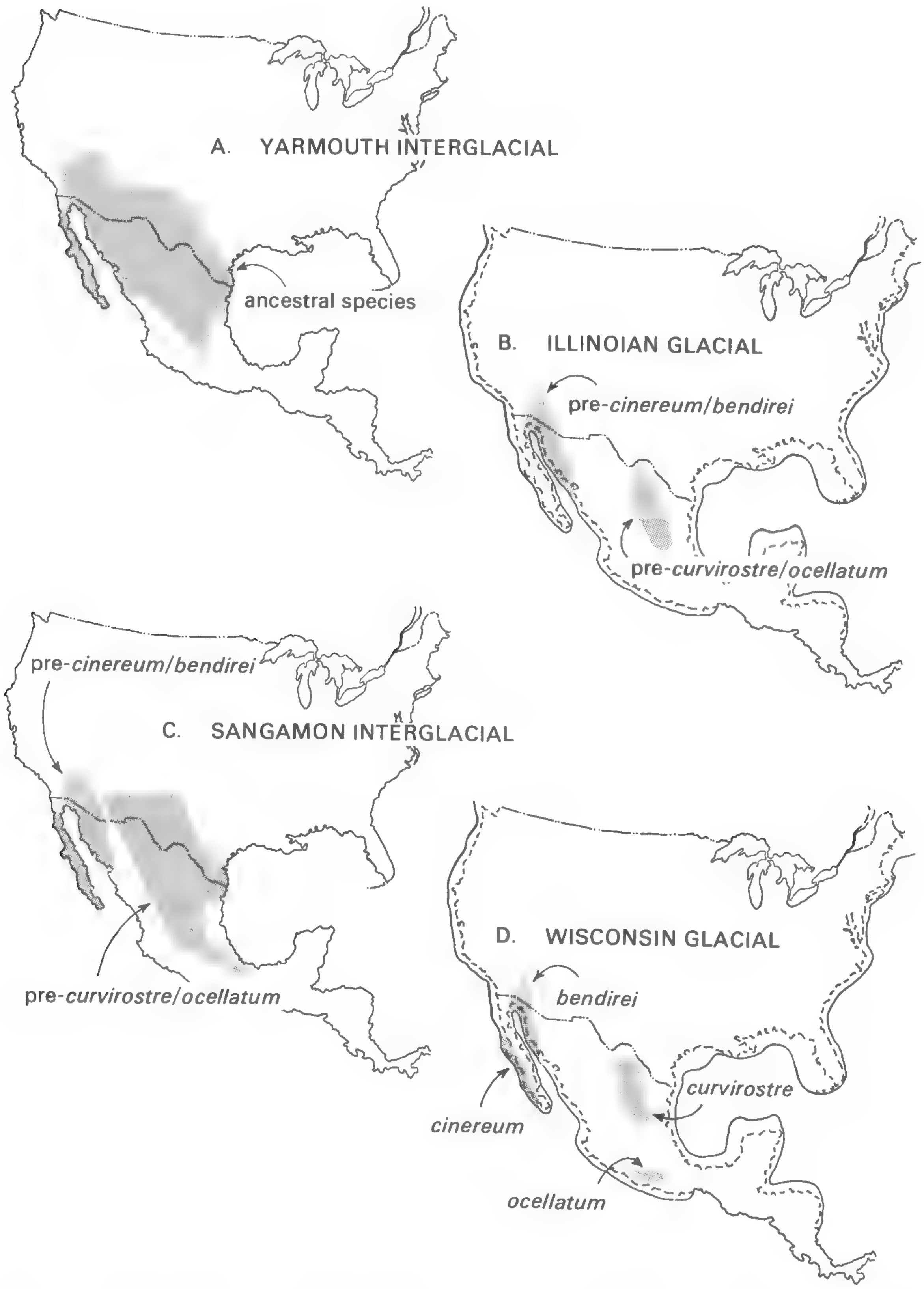

A. YARMOUTH INTERGLACIAL
ancestral species
B. ILLINOIAN GLACIAL
pre-cinereum/bendirei
pre-curvirostre/ocellatum
pre-cinereum/bendirei
C. SANGAMON INTERGLACIAL
pre-curvirostre/ocellatum
D. WISCONSIN GLACIAL
bendirei
curvirostre
cinereum
ocellatum

Figure 7. Possible mode of differentiation of the Curve-billed Thrasher (*Toxostoma curvirostre*) complex, showing two glacial cycles required and postulated refugial origins.

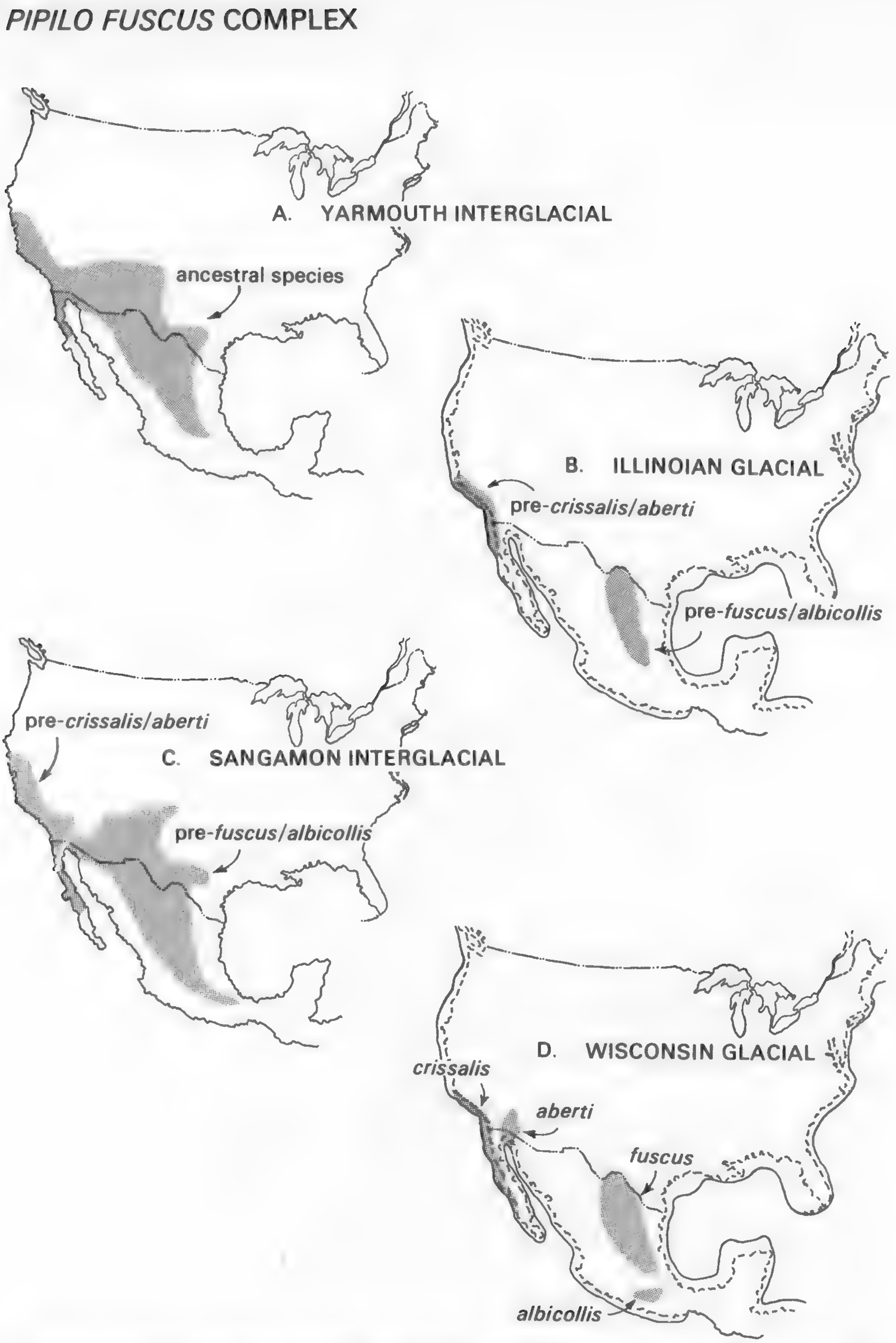

PIPILO FUSCUS COMPLEX
A. YARMOUTH INTERGLACIAL
ancestral species
B. ILLINOIAN GLACIAL
pre-crissalis/aberti
pre-fuscus/albicollis
pre-crissalis/aberti
C. SANGAMON INTERGLACIAL
pre-fuscus/albicollis
D. WISCONSIN GLACIAL
crissalis
aberti
fuscus
albicollis

Figure 8. Possible mode (two-stage version) of differentiation of the Brown Towhee (*Pipilo fuscus*) complex, showing postulated refugial origins.

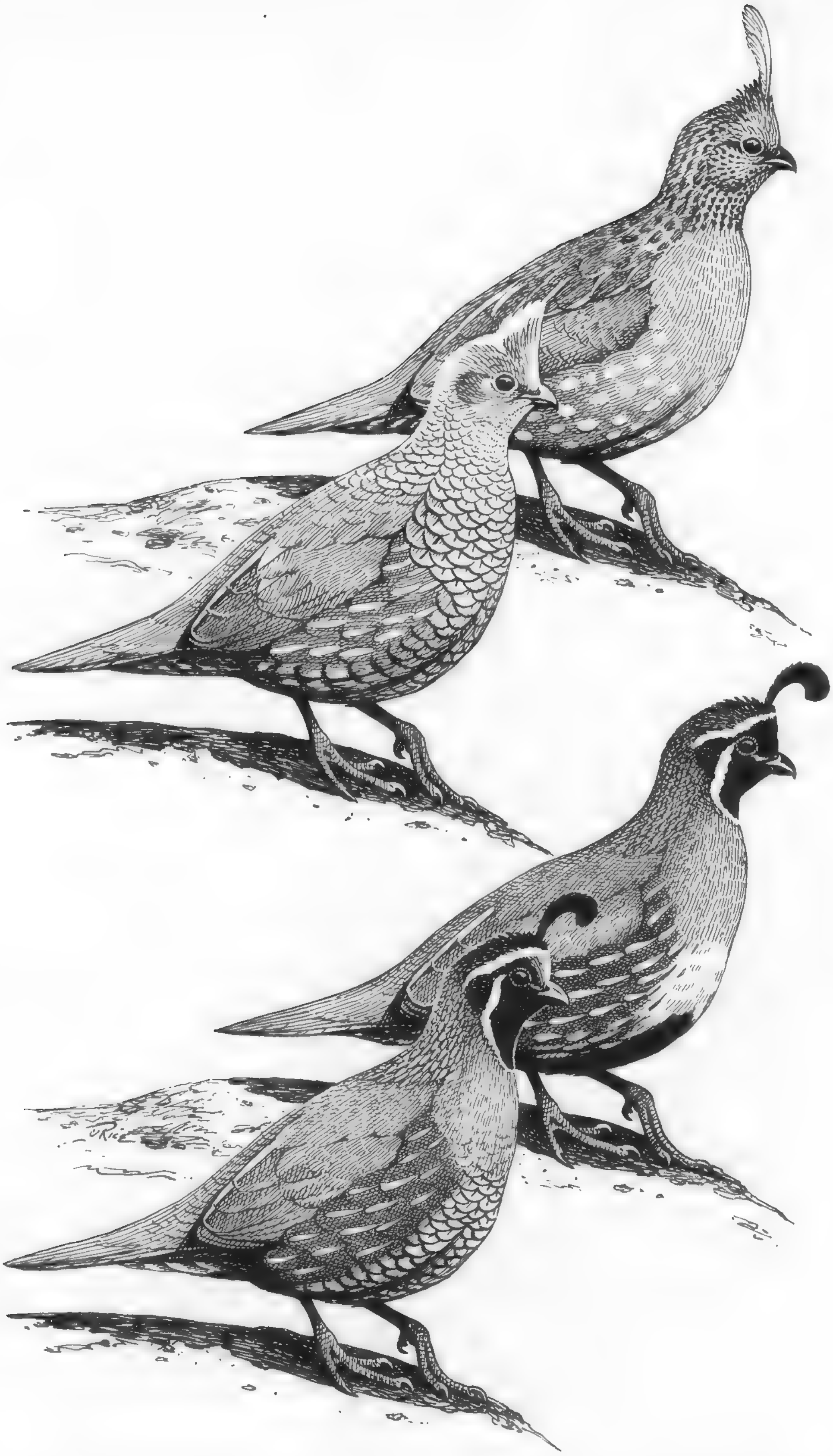
As in the single-cycle model, we begin with a relatively widespread ancestral towhee. That species may have become disjoined, perhaps in the Illinoian glaciation, into two populations: pre-*crissalis/aberti* in the Californian Refugium and pre-*fuscus/albicollis* in the Chihuahuan Refugium (Figure 8). With deglaciation, pre-*crissalis/aberti* may have spread eastward into the Mohave Desert while pre-*fuscus/albicollis* spread west into Baja California (south or east of pre-*crissalis/aberti*) and into southern Mexico. With the Wisconsin glaciation, the pre-*crissalis/aberti* segment in the Mohave Desert may have been pinched off into the Sonoran Refugium, where it became *aberti* as the Wisconsin progressed. At the same time, the Baja California segment of pre-*fuscus/albicollis* probably became isolated in the southern part of the Californian Refugium, in contact, and interbreeding, with pre-*crissalis* from the north. This could have led to the *albigula* population that exists in Baja California today. Meanwhile, the other segment of pre-*fuscus/albicollis* probably became fragmented into isolates in the Chihuahuan and Balsan Refugia. This would have led to *fuscus* arising in the former and *albicollis* in the latter.

This more complicated model fits the sequence of relationships proposed by Davis (1956) and Marshal (1964), and perhaps is more accurate. On the other hand, a single-cycle origin may also be plausible, in spite of the apparently intermediate nature of *albigula* of Baja California. It is possible that the approach there of *crissalis* toward *fuscus* is not due to actual intergradation, but merely reflects a retention or independent evolution of similar plumage patterns.

### Scaled Quail Complex

This complex consists of four species, which I place in the genus *Callipepla* (which includes *Lophortyx*): California ( *C. californica*), Gambel's (*C. gambelii*), Elegant (*C. douglasii*) and Scaled (*C. squamata*) Quails. The ranges of the species are such that several species are sympatric to some degree, but *californica* is essentially allopatric (Figure 6). This complex almost certainly evolved in a multicyclic way, probably involving two glacial ages. During the first cycle a widespread ancestor probably became disjoined into three refugial isolates (Figure 9): Californian (pre-*californica/gambelii*), Sonoran-Sinaloan (pre-*douglasii*), and Chihuahuan (pre-*squamata*). With deglaciation, pre-*californica/gambelii* probably expanded into the northern Sonoran Aridlands, coming in contact with the more southern pre-*douglasii*. With a return of glaciation, this eastern arm of pre-*californica/gambelii* became disjoined and isolated in the Sonoran Refugium, evolving into *gambelii* and pushing *douglasii* southward into the Sinaloan Refugium. Westward, in the Californian Refugium, *californica* would have evolved simultaneously with *gambelii* and *douglasii*, while *squamata* was reaching final differentiation in its ancestral Chichuahuan Refugium. The age of *californica* and *gambelii* as species could thus be Wisconsin, while *douglasii* and *squamata* may have differentiated as species in the Illinoian glaciation.

Related to the *Callipepla* complex are quail of the genus *Colinus*, consisting of three allopatric neotropical species — Black-throated Bobwhite (*C. nigrogularis*), Spot-bellied Bobwhite (*C. leucopogon*), and Crested Bobwhite (*C. cristatus*) — as well as the more widely ranging Common Bobwhite (*C. virginianus*), which is divisible into the *virginianus* subspecies group (largely in the United States) and the *coyolcos* subspecies group



The Scaled Quail complex. From top to bottom: the Elegant Quail (*Callipepla douglasii*), Scaled Quail (*C. squamata*), Gambel's Quail (*C. gambelii*), and California Quail (*C. californica*). Drawing by Orville O. Rice.

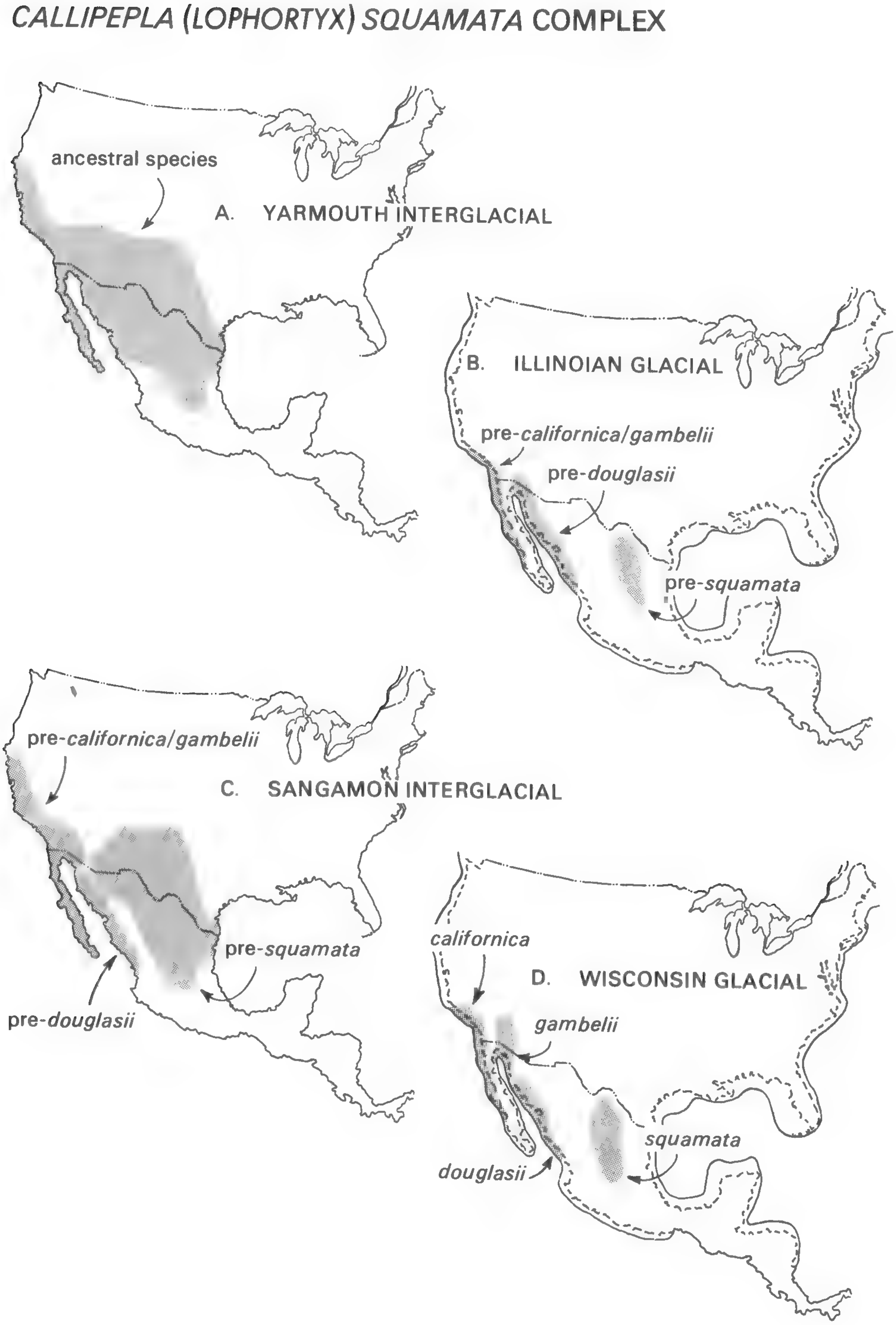

CALLIPEPLA (LOPHORTYX) SQUAMATA COMPLEX
ancestral species
A. YARMOUTH INTERGLACIAL
B. ILLINOIAN GLACIAL
pre-californica/gambelii
pre-douglasii
pre-squamata
pre-californica/gambelii
C. SANGAMON INTERGLACIAL
pre-squamata
pre-douglasii
californica
D. WISCONSIN GLACIAL
gambelii
squamata
douglasii

Figure 9. Possible mode of differentiation of the Scaled Quail (*Callipepla squamata*) complex, showing two glacial cycles required and postulated refugial origins.

(largely in Mexico). *Virginianus, coyolcos,* and perhaps *nigrogularis,* may have arisen from the fregmentation of a single ancestral species during a recent glaciation, differentiating probably in a refugium in Florida (*virginianus*), southern Mexico — perhaps in the southern Isthmus of Tehuantepec (*coyolcos*), and Yucatan (*nigrogularis*). With deglaciation, *coyolcos* stock spread northward on the Pacific slope to Arizona and Sonora (now *C. v. ridgwayi*) and on the Atlantic slope to Tamaulipas where it intergrades (as *C. v. aridus*) with the westwardly expanded *virginianus* group (Aldrich, 1942). The differentiation of *C. leucopogon* and *C. cristatus* may also fit this sequence of events, but I have not investigated the possibilities.

## Other Southwestern Aridlands Forms

Six other species in the aridlands avifauna appear to have originated in refugia of the Southwestern Aridlands; they are listed in Table 2 along with species already discussed.

Worthen's Sparrow (*Spizella wortheni*). — The nearest relative of *Spizella wortheni,* which is endemic to the Mexican Plateau, is generally considered to be the Field Sparrow (*S. pusilla*) of eastern North America. I postulate that their common ancestor once ranged from the eastern United States to northern Mexico and that during a glacial interval it became separated into two isolates. As a consequence, *wortheni* probably arose in the Chihuahuan Refugium and *pusilla* in the Florida Refugium, perhaps as recently as the Wisconsin glaciation (Figure 10).

Cassin's Sparrow (*Aimophila cassinii*). — A member of the Bachman's Sparrow (*A. aestivalis*) complex, *cassinii* could have arisen as recently as the Wisconsin glaciation (Figure 10) through a single fragmentation of a wide-ranging ancestor. Accordingly, *cassinii* probably arose in the Chihuahuan or Gulf Refugium, *aestivalis* in the Florida Refugium, *botterii* in southern Mexico (perhaps in the Tehuantepec Refugium), and *petenica* possibly in the Yucatan Refugium.

Mexican Duck (*Anas* [*platyrhynchos*] *diazi*). — As in the above example, *diazi* has relatives in eastern North America, but its relationship to the holarctic Mallard (*A. platyrhynchos*), with which it interbreeds, complicates the analysis. Johnsgard (1961) studied the complex, including its relationships and possible history, and ranks the forms in order of relationship as follows: *platyrhynchos, diazi, fulvigula* (Mottled Duck), and *rubripes* (Black Duck). Using this sequence, I postulate a somewhat different mode of differentiation than that proposed by Johnsgard. First, I visualize an ancestral species having achieved a circumpolar range during an interglacial, followed by glacial fragmentation into Old World (pre-*platyrhynchos*) and New World (pre-*rubripes*) populations. Following deglaciation, pre-*platyrhynchos* spread back into the New World, where it occupied the region from the Great Plains westward. With a return of glaciation, pre-*platyrhynchos* may again have been fragmented into Old and New World segments, with the latter destined to give rise to *diazi/fulvigula.* This pre-*diazi/fulvigula* isolate may have become confined initially to the area from Florida westward along the Gulf Coast to eastern Mexico and then up the

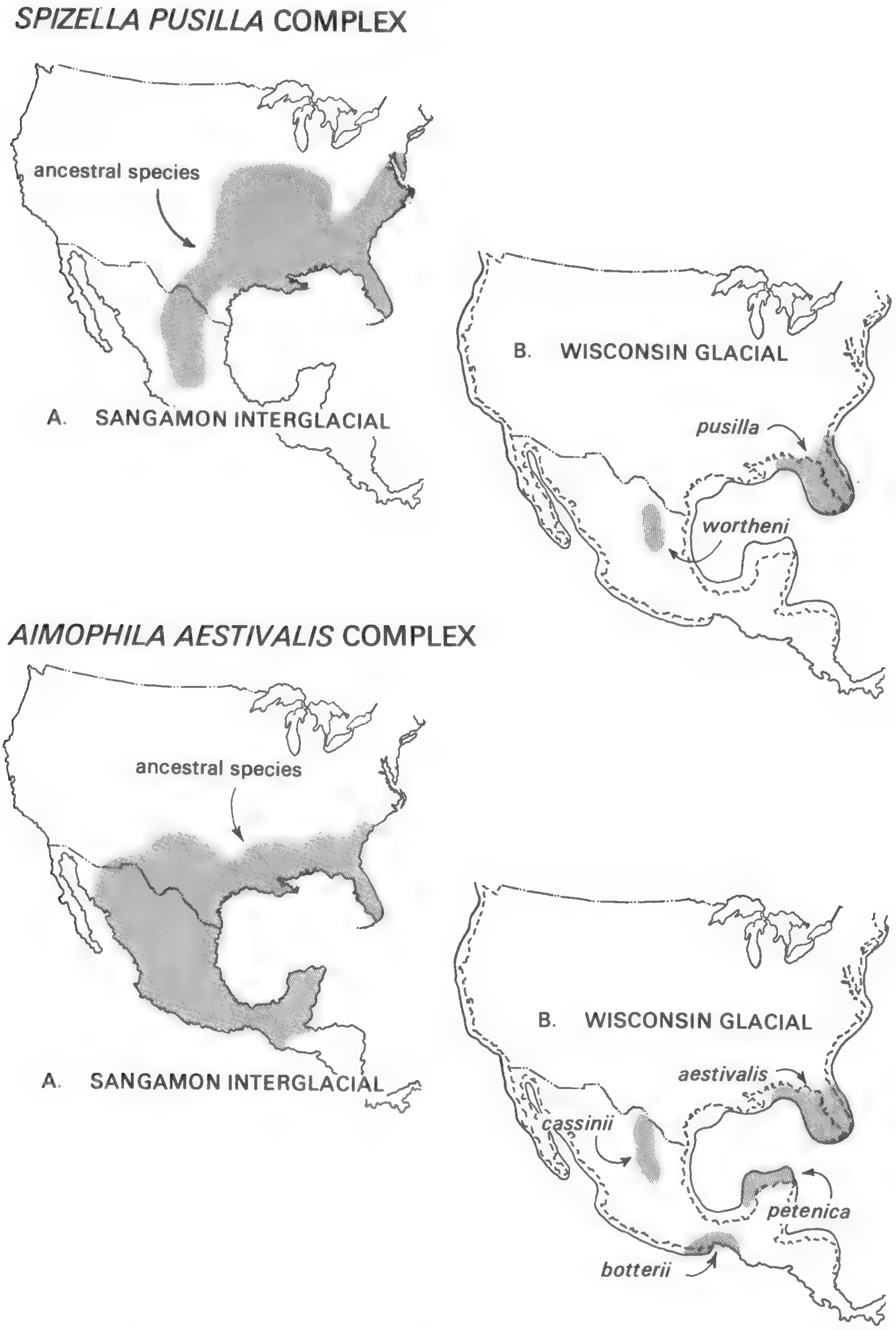

SPIZELLA PUSILLA COMPLEX
ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
pusilla
wortheni
AIMOPHILA AESTIVALIS COMPLEX
ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
aestivalis
cassinii
petenica
botterii

Figure 10. *Upper*, possible mode of differentiation of the Field Sparrow (*Spizella pusilla*) complex, showing postulated refugial origins. *Lower*, possible mode of differentiation of the Bachman Sparrow complex (*Aimophila aestivalis* and its relatives), showing postulated refugial origins.

Rio Grande onto the Mexican Plateau. Meanwhile pre-*rubripes* may have retreated into the southeastern United States. With increased spread of woodland and other ecological barriers, pre-*diazi* probably became isolated in the Chihuahuan Refugium and *fulvigula* in the Gulf Refugium. At the same time, *rubripes* probably achieved its final differentiation in the forested and eastern coastal areas of the southeastern United States. The population that became *platyrhynchos* probably was confined to the area from Beringia westward during that glacial interval, spreading southward and eastward into North America during the Recent period.

This model thus places the split between the precursors of present *platyrhynchos* and *rubripes* at the Illinoian glaciation, with *diazi* and *fulvigula* splitting off from pre-*platyrhynchos* in the Wisconsin. Other models might also account for the differentiation in this complex, including a single fragmentation during glaciation, but the two-staged one conforms with relationships as outlined by Johnsgard (1961).

Costa's Hummingbird (*Archilochus* [*Calypte*] *costae*). — The origin of this hummingbird seems straightforward, but its relationships are more difficult to account for. I suspect that its nearest relative is not Anna's Hummingbird (*A.* [*Calypte*] *anna*) but is the Black-chinned Hummingbird (*Archilochus alexandri*). Whatever the case, *costae* probably arose in the Sonoran Refugium during a glacial interval, perhaps in the Wisconsin. The place of origin of *A. alexandri* is obscure, but that of the related Ruby-throated Hummingbird (*A. colubris*) is probably the southeastern United States (Florida Refugium). Almost certainly, if *anna* arose during a glacial interval, it would have been in the Californian Refugium.

Gilded Flicker (*Colaptes chrysoides*). — This flicker interbreeds with the Red-shafted Flicker (*C. cafer* [*auratus*]) and is probably conspecific with it (Short, 1965). *Chrysoides* is confined to the lowlands, with *cafer* replacing it at higher elevations in forested areas. It is difficult to see how *chrysoides* could have been separated from *cafer* during a glacial interval, because then, as now, desert probably intergraded with montane forest through riparian woodland. I suspect that the two may never have been completely isolated from each other, but were probably segregated — and continue to be — to a sufficient degree to allow divergence. *Chrysoides* and *cafer* are more closely related to each other than either is to *auratus*, according to Short (1965), which suggests a later divergence of the first two. *Chrysoides* probably arose in the Sonoran-Sinaloan Refugium.

Lucy's Warbler (*Vermivora luciae*). — This warbler has several close relatives, including Virginia's Warbler (*V. virginiae*) of the southwestern United States, Colima Warbler (*V. crissalis*) of the Mexican Plateau, and Nashville Warbler (*V. ruficapilla*) of northern and central-western North America. Differing views of the relationships among the group hamper the reconstruction of possible evolutionary histories of these species. Mengel (1964) set *luciae* apart on the basis of its rather divergent habitat, small size, and nesting habits; but in song, call notes, and plumage it is much like *virginiae*. The habitat of *luciae* is unique among the species of *Vermivora*, but this, in itself, is not necessarily of any taxonomic significance. In size, *luciae* is about as small compared to *virginiae* as *crissalis* is large, so that

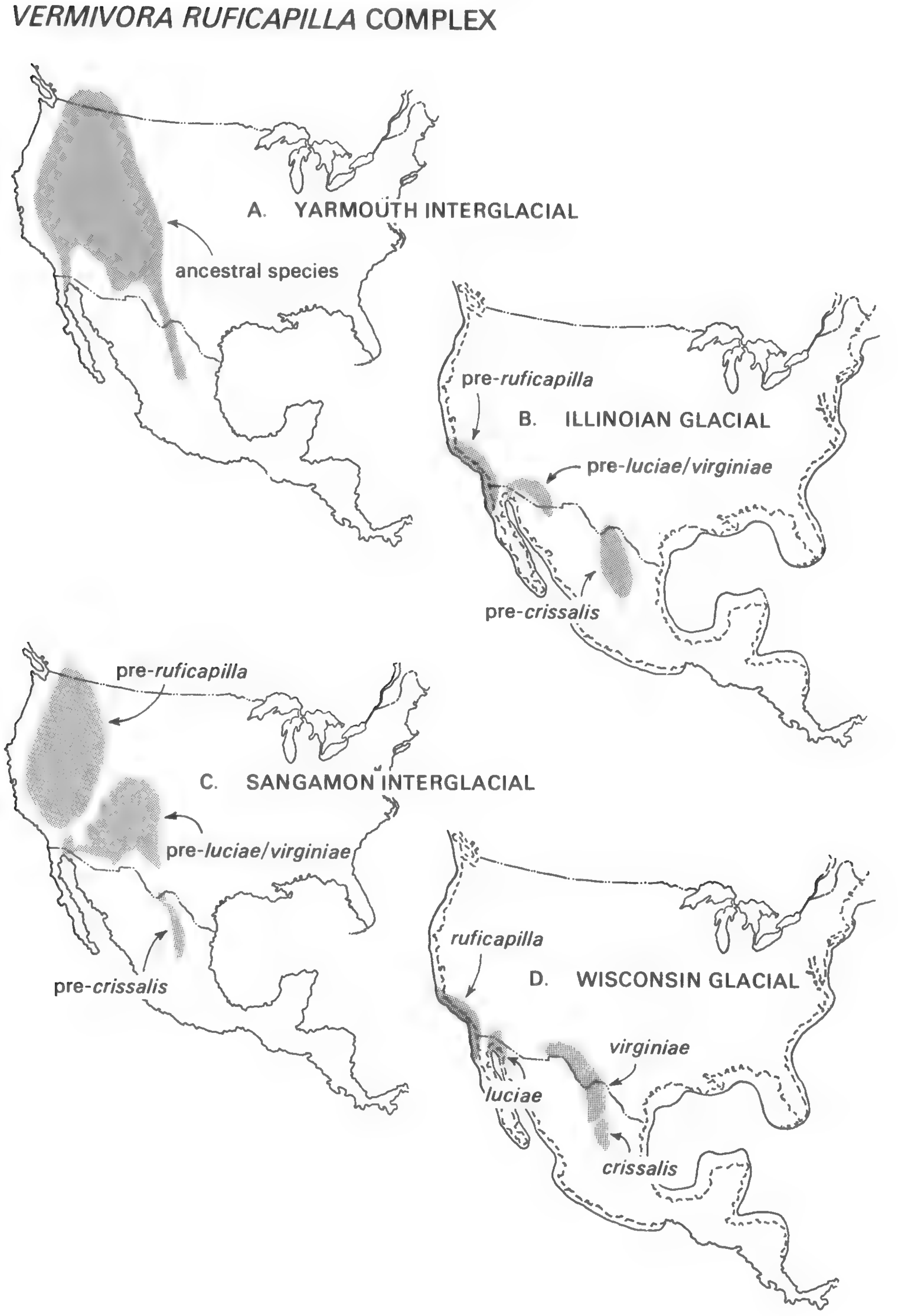

VERMIVORA RUFICAPILLA COMPLEX
A. YARMOUTH INTERGLACIAL
ancestral species
B. ILLINOIAN GLACIAL
pre-ruficapilla
pre-luciae/virginiae
pre-crissalis
C. SANGAMON INTERGLACIAL
pre-ruficapilla
pre-luciae/virginiae
pre-crissalis
D. WISCONSIN GLACIAL
ruficapilla
virginiae
luciae
crissalis

Figure 11. Possible mode of differentiation of the Nashville Warbler complex (*Vermivora ruficapilla* and its relatives), showing two glacial cycles required and postulated refugial origins.

*crissalis* might just as well be singled out as divergent in this regard. Furthermore, size in *luciae* may be dictated by physiological and other considerations (see "Phillips Law," Phillips, *et al.*, 1964) just as its nesting habits may be. *Luciae* nests in holes and crevices above ground, unlike the others of this complex, which nest on the ground. However, *luciae* nests in the spring and early summer prior to the major rains in the Southwest. Thus, it may avoid ground-nesting because the sparse vegetation at that time of the year would expose the eggs and young to high temperatures and to predators. For the reasons mentioned above, I see no reason to consider *luciae* aberrant and I link it closely to *virginiae*.

As I see it, the ancestral species of this complex may have inhabited montane shrubland and achieved a wide range in western North America during an interglacial (Figure 11). Subsequently, probable fragmentation occurred during a glacial interval, with the following isolates resulting: pre-*ruficapilla* in or near the Californian Refugium, pre-*luciae/virginiae* in the Sonoran Refugium, and pre-*crissalis* in the Chihuahuan Refugium. During the succeeding interglacial, pre-*luciae/virginiae* may have spread eastward, only to be fragmented into two isolates during the next glacial interval. During that second interval, *virginiae* may have arisen in the Chihuahuan Refugium, *luciae* in the Sonoran Refugium, while *ruficapilla* achieved final speciation in the Californian Refugium and *crissalis* in the Chihuahuan Refugium. The presumed sympatry, or near-sympatry, of *virginiae* and *crissalis* during the second glacial interval might explain the origin of notable difference in song of these otherwise similar, and now allopatric, species. *Ruficapilla* presumably spread into eastern North America during the Recent Epoch, resulting today in two allopatric, but weakly demarked, races on the continent.

## *Less Defined Evolutionary Histories*

Several other species or semi-species of birds may have originated in the Southwestern Aridlands, but the details of their possible evolutionary histories are less apparent than those of most of the forms already discussed. Nevertheless, I postulate that the bulk of these forms originated in glacial-age refugia and are thus of Pleistocene age. Furthermore, because of desert scrub requirements, I surmise that most of these arose in the Sonoran (or Sonoran-Sinaloan) Refugium, while other contemporaries were evolving in refugia outside the Southwestern Aridlands. Species possibly originating in the Sonoran (or Sonoran-Sinaloan) Refugium include the Roadrunner (*Geococcyx californicus*), Gila Woodpecker (*Centurus uropygialis*), Black-tailed Gnatcatcher (*Polioptila melanura*), Bell's Vireo (*Vireo bellii*), Pyrrhuloxia (*Cardinalis sinuatus*), Varied Bunting (*Passerina versicolor*), Black-throated Sparrow (*Amphispiza bilineata*), Rufous-winged Sparrow (*Aimophila carpalis*), and the aforementioned Cactus Wren (Table 2). Several of these bear further discussion.

*Geococcyx.* — The genus *Geococcyx* is known from three species: Greater Roadrunner (*G. californianus*), Lesser Roadrunner (*G. velox*), and the extinct *G. conklingi*. All of these species may have arisen from a common ancestor in a single glacial interval, perhaps as recently as the Wisconsin. I suggested the area of origin of *californianus* as the Sonoran Refugium, while *velox* may have arisen in the Balsan or Tehuantepec Refugium. *Conklingi* is known only from late Pleistocene-early Recent deposits in New Mexico and Nuevo Leon (Westmore, 1956), which suggest an origin in the Chihuahuan Refugium.

*Polioptila.* — The gnatcatchers are primarily a neotropical genus. The nearest relatives of the Black-tailed Gnatcatcher (*P. melanura*) may be the Tropical Gnatcatcher (*P. plumbea*) and (*P. albiloris*). Within *melanura* there are two groups: *californica* subspecies in southwestern California and *melanura* and other subspecies in Baja California and to the east. *Californica* may have arisen during the Wisconsin glacial from an isolate of what was, during the last (Sangamon) interglacial, a westward arm of a Sonoran species.

*Dendrocopos.* — Also originating in this way may have been Nuttall's Woodpecker (*Dendrocopos nuttallii*) in non-desert shrubland and woodland of the Californian Refugium. Its nearest relative seems to be the Ladder-backed Woodpecker (*D. scalaris*), a widespread species of arid and semiarid habitats of the Southwest and Central America. The area of origin of *scalaris* is unclear because the species is so widespread; it may have arisen in the Sonoran, Balsan, Tehuantepec, or even a Central American refugium.

*Amphispiza.* — The evolution of the two species of *Amphispiza,* the Black-throated Sparrow (*A. bilineata*) and the Sage Sparrow (*A. belli*), seems to be more complicated. In the first cycle, a common ancestor could have become fragmented into two isolates, pre-*belli* in the Californian Refugium and pre-*bilineata* in the Sonoran Refugium (Figure 12). Pre-*belli* would have been a species of chaparral and pre-*bilineata* a species of desert shrublands. With deglaciation, pre-*belli* spread eastward into the sagebrush shrubland of the Great Basin, which it now shares in the southern portion with *bilineata.* With a second glacial interval, pre-*belli* may have fragmented into two isolates, one in the Californian Refugium and one in the Great Basin Refugium. The former would have become *A. b. belli* and the latter *A. belli nevadensis.* On recontact in the Recent Period, the two might have interbred and produced the intergrade *A. belli canescens.* A simpler model would involve only one cycle, with the Great Basin range of *belli* and its races being of Recent origin. This also could apply to the *californica* group of *Polioptila melanura.*

## Evolutionary Interaction with Adjacent Areas

So far, very little evolutionary interaction has been revealed between the Southwestern Aridlands and two northern regions, the Great Basin and the Great Plains. I discern only the possible *Amphispiza* interaction, mentioned above, between the former and the Great Basin, while only one or two cases seem to exist between the Southwestern Aridlands and the refugia of the Great Plains. Besides the *Anas platyrhynchos* complex and possibly the *Aimophila cassinii* complex, the only other case may be that of the Prairie Grouse complex, *Tympanuchus cupido.* Several forms of this grouse existed in Recent times in North America, including *cupido, pinnatus, attwateri,* and *pallidicinctus.* Perhaps during an interglacial, the ancestor of this group

*AMPHISPIZA* COMPLEX

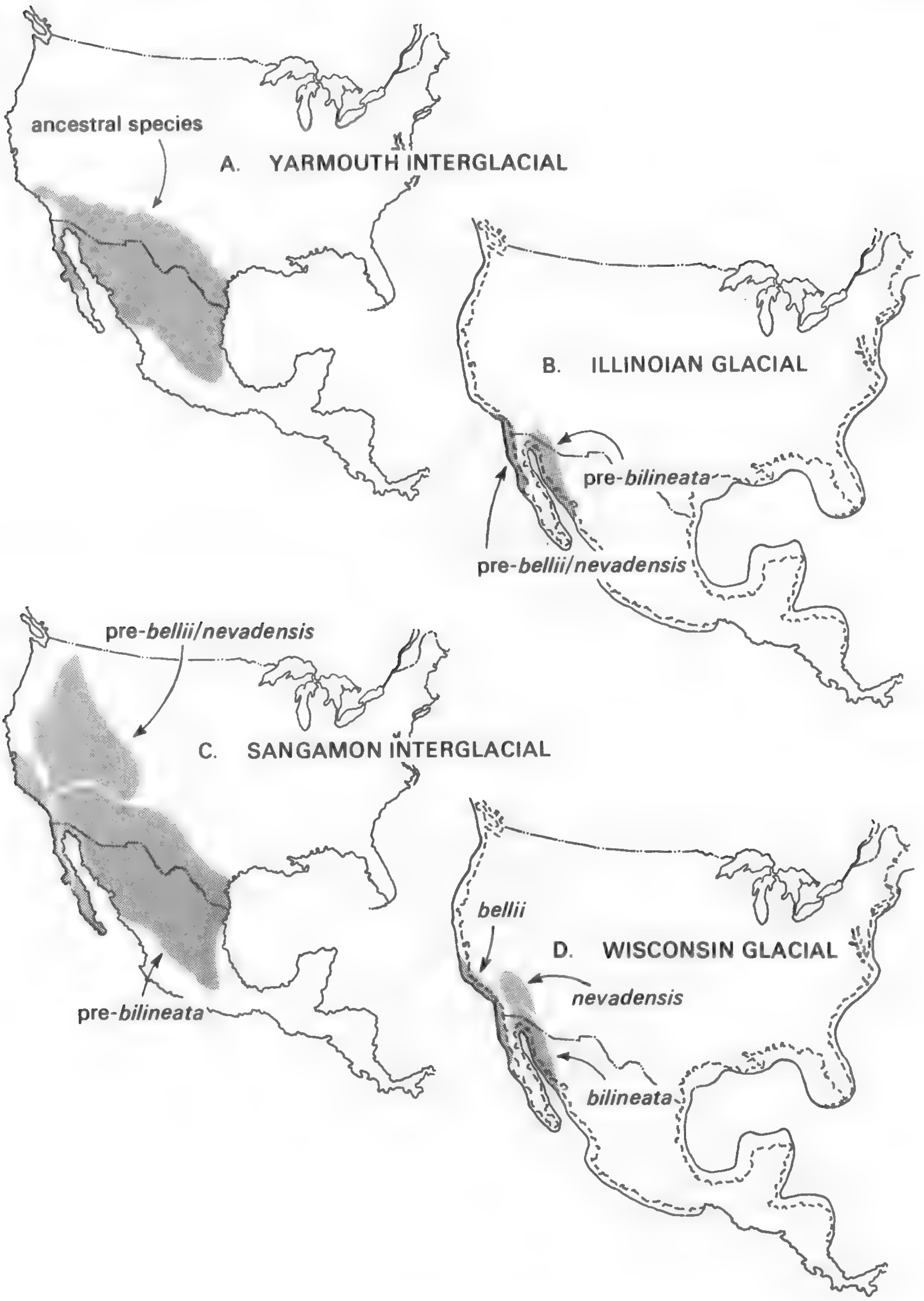

ancestral species
A. YARMOUTH INTERGLACIAL
B. ILLINOIAN GLACIAL
pre-*bilineata*
pre-*bellii/nevadensis*
pre-*bellii/nevadensis*
C. SANGAMON INTERGLACIAL
pre-*bilineata*
*bellii*
D. WISCONSIN GLACIAL
*nevadensis*
*bilineata*

Figure 12. Possible mode of differentiation of the Sage and Black-throated Sparrows (genus *Amphispiza*), showing two glacial cycles required and postulated refugial origins. An alternative would require only one glacial cycle (A and B), with *nevadensis* (a race of *belli*) arising in the Recent Period and without refugial isolation.

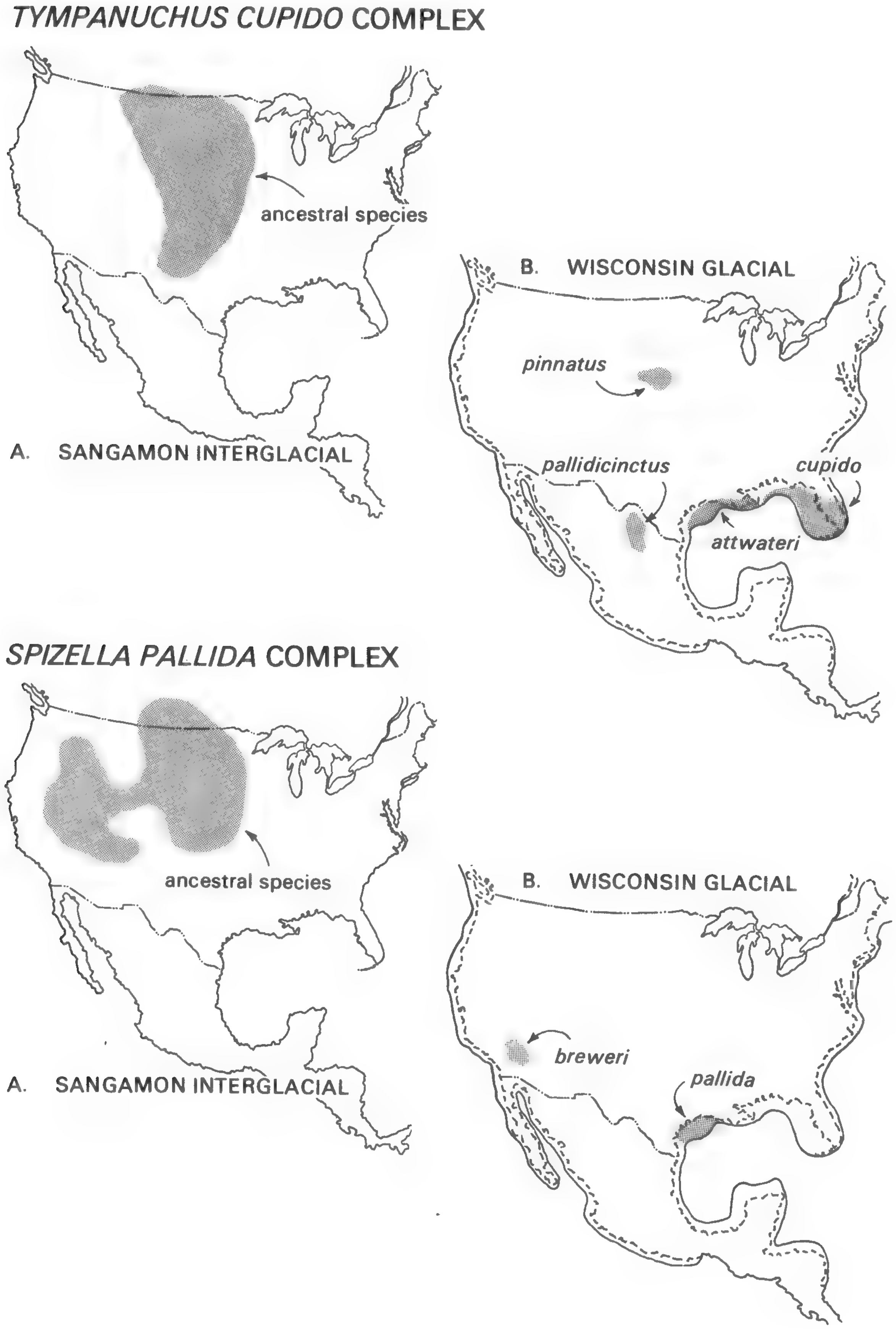

TYMPANUCHUS CUPIDO COMPLEX
ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
pinnatus
pallidicinctus
cupido
attwateri
SPIZELLA PALLIDA COMPLEX
ancestral species
A. SANGAMON INTERGLACIAL
B. WISCONSIN GLACIAL
breweri
pallida

Figure 13. *Upper*, possible mode of differentiation of the Prairie Grouse complex (genus *Tympanuchus*), showing postulated refugial origins. *Lower*, possible mode of differentiation of the Clay-colored Sparrow complex (*Spizella pallida* and *S. breweri*), showing postulated refugial origins.

achieved a wide range in the Great Plains and vicinity, only to be fragmented into several isolated populations during a glacial interval (Figure 13). As a result, *pinnatus* may have arisen in the Nebraskan Refugium, *attwateri* in the Gulf Refugium, and *pallidicinctus* in the Chihuahuan Refugium. The last two forms thus probably arose from populations retreating southward from the southern Plains. *Cupido* may have originated from a population that is known to have been in Florida in the late Pleistocene (Ligon, 1965), perhaps arriving there along xeric vegetation bordering the Gulf of Mexico. With deglaciation, *cupido* and *pallidicinctus* may have spread northward and away from their centers of origin, while *pinnatus* expanded in various directions. *Attwateri* became isolated on the Texas-Louisiana Coast with other prairie elements, where it remains as a prairie relict today.

In summary, Pleistocene differentiation involving birds of the Southwestern Aridlands seems to have centered in the Californian, Sonoran, Chihuahuan, and Balsan refugia, postulated to have existed during glacial intervals in North America. Lesser degrees of evolutionary interaction are postulated to have involved other areas, notably the refugia of the Great Basin, Great Plains, southeastern United States, and Central America.

## *Differentiation of the Avifauna of the Great Plains and Associated Areas*

Although many of the discernable evolutionary interactions with the avifauna of the Great Plains involved the Beringia Refugium (or the Old World), some other areas also seem to have been involved. I pointed out that the avifaunas of the refugia in the Southwestern Aridlands and the Great Plains probably interacted in the evolution of only two or three groups: *Anas platyrhynchos* complex, *Tympanuchus cupido* complex, and possibly *Aimophilia cassinii* complex. Limited interactions also occurred between the avifaunas of the Great Plains and the Great Basin, although this is somewhat unexpected in view of all of the species shared at present between the two (Table 1). Only in the genus *Spizella* does fragmentation and isolation seem to have occurred in a species ancestrally shared between the two areas. The result is that Brewer's Sparrow (*S. breweri*) probably arose in the Great Basin Refugium and the Clay-colored Sparrow (*S. pallida*) in the Nebraskan Refugium (Figure 13).

The evolutionary relationships between the avifaunas of the Great Plains and higher-latitude area, are suggested by the existence of several pairs of replacement species found in the two regions. To illustrate how the interaction may have taken place, we may use a modern species such as the Snow Bunting (*Plectrophenax nivalis*). This species breeds circumpolarly in arctic tundra, but if glaciation were to recur, the range would be drastically altered (Figure 14). In North America, the Snow Bunting would be forced out of much of the arctic, but could probably survive in the Beringian Refugium, and thence westward through Eurasia. Birds breeding there during the Pleistocene might have been resident, but more likely they migrated southward in winter. The most logical migratory pathway carried them through eastern Siberia, which was largely ice-free (Flint, 1971), into Eurasia. At one time I thought small passerines breeding in Beringia might have wintered in the Americas, but this migration route probably would have been extremely difficult for birds (Mengel, 1970). At any rate, another population of Snow Bunting might be pushed southward ahead of glaciers into central North America, occupying periglacial tundra. The northern Great Plains might have afforded the best environment for high-latitude species in the Pleistocene, in the region from the Nebraskan Refugium northward. There, habitats probably ranged from tundra to prairie, and perhaps in time a species could have shifted its habitat requirements from the former to the latter. In this way, a prairie species could have arisen from an isolated population of a tundra bird, while farther north any other isolate might have remained tundra-oriented. After deglaciation the Beringia isolate could have expanded eastward and southward to occupy the available tundra habitat, while the southern isolate remained in the prairie. The rapidly spreading boreal forest would have re-enforced the separation of the two species, acting as a barrier between the two and preventing recontact. Could it be that in *Plectrophenax* itself such a sequence of events might actually have produced a near relative at some time during the Pleistocene, such as the Lark Bunting (*Calamospiza melanocorys*)? If, as suggested by Paynter (1970), *Calamospiza* is closely related to *Plectrophenax,* then indeed the model discussed above may have involved this group; however, evidence of any close relationships between *Plectrophenax* and *Calamospiza* still remains to be published.

More clear-cut examples that seem to reflect this type of evolutionary interaction include such Great Plains species as the Ferruginous Hawk (*Buteo regalis*), Marbled Godwit (*Limosa fedoa*), and Chestnut-collared Longspur (*Calcarius ornatus*), derived from the same ancestors as the arctic Rough-legged Hawk (*Buteo lagopus*), Bar-tailed Godwit (*Limosa lapponica*) and Lapland Longspur (*Calcarius lapponicus*). The *Calcarius ornatus-lapponicus* complex illustrates especially well how this type of differentiation may have come about (Figure 15). The Long-billed Curlew (*Numenius americanus*) of the Great Plains also seems to fit here, although its near relatives, the Eurasian (*N. arquata*) and Far Eastern (*N. madagascariensis*) Curlews have not reinvaded the New World. Conceivably the White-necked Raven (*Corvus cryptoleucus*) may also fit this model, although its exact area of origin is obscure (Chihuahuan Refugium?) and its holarctic counterpart, the Common Raven (*C. corax*), has a wide subarctic range in both North America and Eurasia. Other more distant pairings are the Prairie Falcon (*Falco mexicana*) and Wilson's Phalarope (*Phalaropus* [*Steganopus*] *tricolor*), with the arctic Gyrfalcon (*F. rusticolus*) and Northern Phalarope (*P.* [*Lobipes*] *lobatus*) and possibly the Red Phalarope (*P. fulicarius*). More distant yet, perhaps to the point of not having any really close relatives, is the Mountain Plover (*Charadrius* [*Eupoda*] *montanus*), which seems to have originated on the Great Plains.

This same general mode of differentiation seems to apply to many birds of coniferous forests and other arboreal habitats. There exist many species endemic to North American forests with near relatives farther north and/or in Eurasia. Such birds probably arose from ancestors that achieved a circumboreal distribution during an interglacial, then were cleaved during glacial intervals into New World and Old World isolates, which then differentiated. Following differentiation there developed a tendency for the Old World form to invade the New World more often than vice versa. The reason for this directional movement could be that Old World species, be-

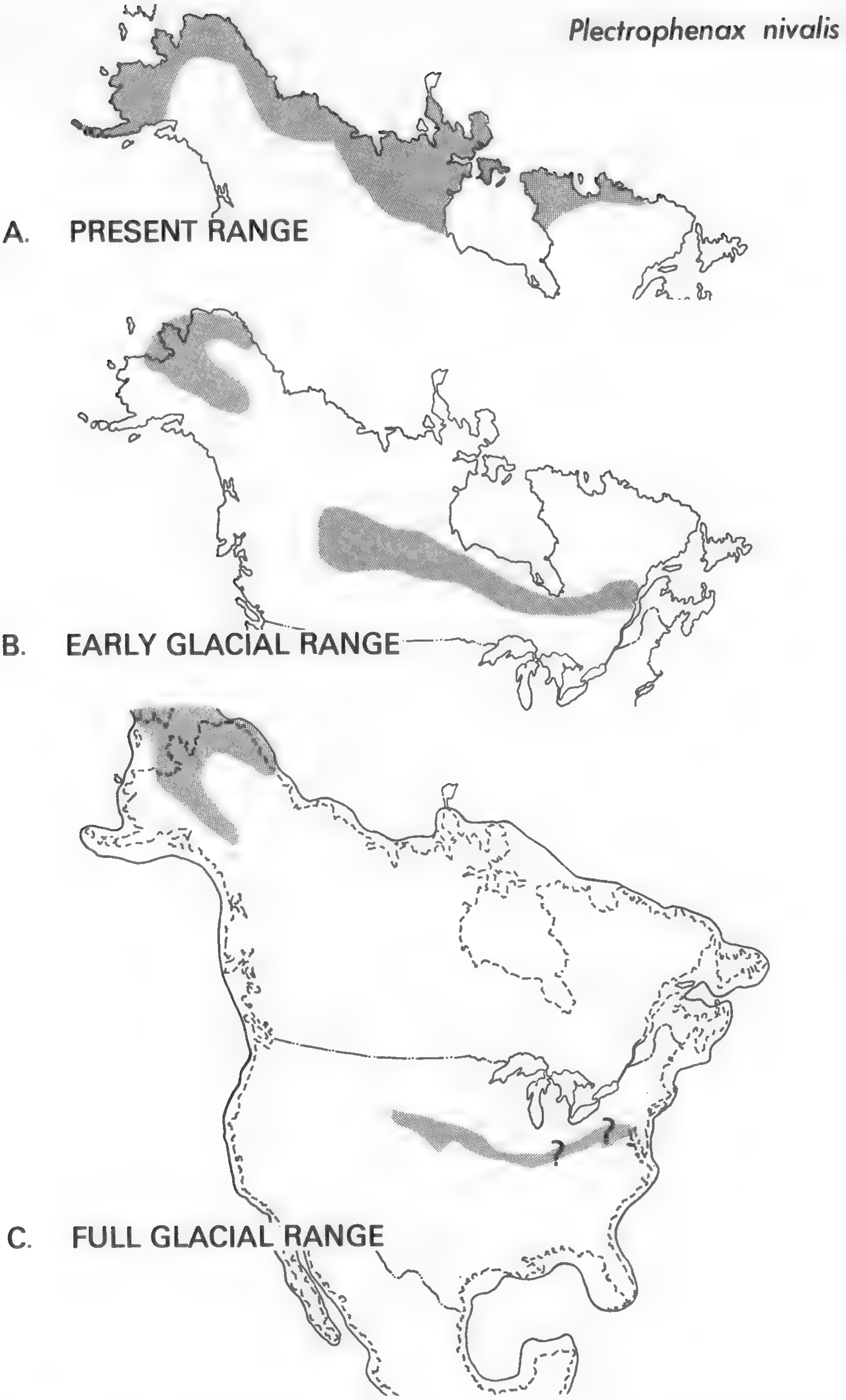

Plectrophenax nivalis
A. PRESENT RANGE
B. EARLY GLACIAL RANGE
C. FULL GLACIAL RANGE
?
?

Figure 14. Postulated alteration in the range of the Snow Bunting (*Plectrophenax nivalis*) that might occur in the face of a future glacial cycle. Note refugial populations in Alaska (and westward) and in the central United States (and possibly eastward).

*CALCARIUS LAPPONICUS* COMPLEX

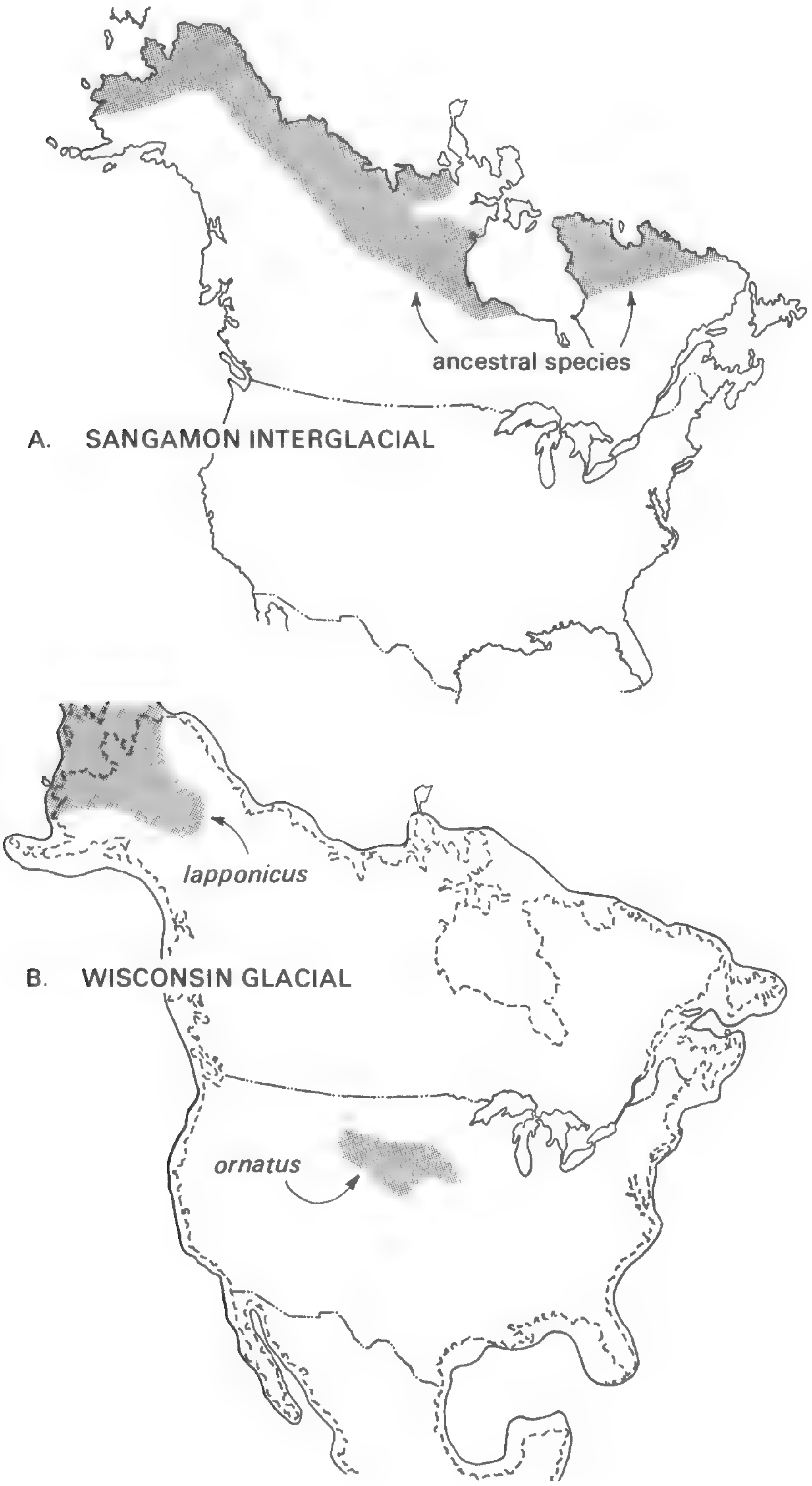

ancestral species
A. SANGAMON INTERGLACIAL
*lapponicus*
B. WISCONSIN GLACIAL
*ornatus*

Figure 15. Possible mode of differentiation of the Lapland Longspur complex (*Calcarius lapponicus* and *C. ornatus*) showing postulated refugial origins.

cause they occurred farther north during glacial intervals, traveled much shorter distances to invade Alaska or the boreal nearctic. Meanwhile, the related North American forms remain southward, trapped or impeded from higher latitudes by the slowly melting glaciers, with later expansion blocked by their congener's presence.

Species or semi-species that may have originated in this way are shown in Table 3. The list is not exhaustive, but it does include such range relationships as (1) intercontinental allopatry, Siberian Jay (*Perisoreus infaustus*) and Gray Jay (*P. canadensis*), (2) intracontinental allopatry, Rough-legged Hawk (*Buteo lagopus*) and Ferruginous Hawk (*B. regalis*), and (3) sympatry on one continent, Northern Three-toed Woodpecker (*Picoides tridactylus*) and Black-backed Three-toed Woodpecker (*P. arcticus*). I did not include cases of sympatry on both continents because of the problem of discerning which species originated on which continent, if indeed they arose in this way, such as the redpolls (*Carduelis*) and the crossbills (*Loxia*). It is likely that some groups represent double intercontinental invasions that produced two or more species on a continent, such as the Wood (*T. glareola*), Solitary (*T. solitaria*), and Green (*T. ochropus*) Sandpipers. In other cases, multiple differentiation may have been intracontinental, such as the Boreal and Chestnut-backed Chickadees, *Parus hudsonicus* and *P. rufescens*, respectively.

While evolutionary interactions involving the Great Plains avifauna have not been limited to northern refugia, the mechanisms of interactions with other areas, except for the few examples cited, are not readily apparent. For example, the plains-endemic Baird's Sparrow (*Ammodramus bairdii*) seems closely related to the widespread North American Grasshopper Sparrow (*A. savannarum*), which is a member of a strictly New World group, the "sharp-tailed" sparrows. While it seems certain that *bairdii* arose in one of the refugia of the Great Plains during a glacial interval, how this came about in conjunction with other sharp-tailed sparrows is problematical.

Several Great Plains species, or genera, occur also in South America, including several with Old World affinities and perhaps origin, such as the harriers (*Circus*), Burrowing Owl (*Speotyto*), Horned Lark (*Eremophila*), and pipits (*Anthus*). Others, such as the meadowlarks (*Sturnella*), have New World relationships. The case of *Anthus* is particularly interesting, in that the endemic Sprague's Pipit (*A. spragueii*) of the Great Plains is the only species of the genus restricted to North America; yet, in South America, one finds eight members of this otherwise Old World group. The affinities of *spragueii* seem undetermined as yet, although Hall (1961) associated the species with the Short-tailed Pipit (*A. furcatus*) of South America. *Spragueii* does resemble *furcatus* in adult plumage, but in morphology of the foot and the juvenal plumage, the two diverge to some degree. Without more information of the relationship of *spragueii*, any model of its possible evolution is premature.

Several forms of the Great Plains avifauna may have arisen in the Gulf Refugium, during a glacial cycle, including the grouse *Tympanuchus cupido attwateri* and possibly Cassin's Sparrow (*Aimophila cassinii*). The Scissor-tailed Flycatcher (*Tyrannus* [*Muscivora*] *forficata*) and the Black-capped Vireo (*Vireo atricapilla*) also may have arisen here, becoming isolated in the Gulf Refugium during a glacial cycle, where they diverged from

## TABLE 3

## Some Species Pairs that may have Differentiated During Glacial Intervals, Showing Probable Areas of Differentiation, Modern Distribution, and Present Geographical Relationships

| *Probable palearctic differentiates* | *Probable nearctic differentiates* | *Modern distribution** | *Present geographical relationships* |
|---|---|---|---|
| *Aythya marila* (Greater Scaup) | *A. affinis* (Lesser Scaup) | holarctic/nearctic | sympatric |
| *Buteo lagopus* (Rough-legged Hawk) | *B. regalis* (Ferruginous Hawk) | holarctic/nearctic | allopatric |
| *Falco rusticolus* (Gyrfalcon) | *F. mexicanus* (Prairie Falcon) | holarctic/nearctic | allopatric |
| *Pluvialis apricaria* (Golden Plover) | *P. dominica* (American Golden Plover) | palearctic/holarctic | allopatric |
| *Numenius arquatus* (Eurasian Curlew) | *N. americanus* (Long-billed Curlew) | palearctic/nearctic | allopatric |
| *Numenius madagascariensis* (Far Eastern Curlew) |  | palearctic/nearctic | allopatric |
| *Limosa lapponica* (Bar-tailed Godwit) | *L. fedoa* (Marbled Godwit) | holarctic/nearctic | allopatric |
| *Phalaropus fulicarius* (Red Phalarope) | *P. tricolor* (Wilson's Phalarope) | holarctic/nearctic | allopatric |
| *Phalaropus lobatus* (Northern Phalarope) |  | holarctic/nearctic | allopatric |
| *Aegolius funereus* (Boreal Owl) | *A. acadicus* (Saw-whet Owl) | holarctic/nearctic | sympatric |
| *Picoides tridactylus* (Northern Three-toed Woodpecker) | *P. arcticus* (Black-backed Three-toed Woodpecker) | holarctic/nearctic | sympatric |
| *Corvus corax* (Common Raven) | *C. cryptoleucus* (White-necked Raven) | holarctic/nearctic | sympatric |
| *Parus cinctus* (Gray-headed Chickadee) | *P. hudsonicus* (Boreal Chickadee) | holarctic/nearctic | allopatric |
|  | *P. rufescens* (Chestnut-backed Chickadee) | holarctic/nearctic | allopatric |
| *Perisoreus infaustus* (Siberian Jay) | *P. canadensis* (Gray Jay) | palearctic/nearctic | allopatric |
| *Perisoreus nigricans* (Szechwan Jay) |  | palearctic/nearctic | allopatric |
| *Nucifraga caryocatactes* (European Nutcracker) | *N. columbiana* (Clark's Nutcracker) | palearctic/nearctic | allopatric |
| *Regulus regulus* (Goldcrest) | *R. satrapa* (Golden-crowned Kinglet) | palearctic/nearctic | allopatric |
| *Regulus ignicapillus* (Firecrest) |  | palearctic/nearctic | allopatric |
| *Bombycilla garrulus* (Bohemian Waxwing) | *B. cedrorum* (Cedar Waxwing) | holarctic/nearctic | sympatric |
| *Bombycilla japonicus* (Japanese Waxwing) |  | palearctic/nearctic | allopatric |
| *Lanius excubitor* (Great Gray or Northern Shrike) | *L. ludovicianus* (Loggerhead Shrike) | holarctic/nearctic | allopatric |
| *Calcarius lapponicus* (Lapland Longspur) | *C. ornatus* (Chestnut-collared Longspur) | holarctic/nearctic | allopatric |
|  | *C. mccownii* (McCown's Longspur) | holarctic/nearctic | allopatric |

*Zoogeographic region to the left of the slash represents the area of probable origin of the palearctic differentiates. The region to the right indicates the probable origin of the nearctic differentiates.

neotropical ancestors. Both are characteristic of, and largely endemic to, scrubby habitats in the southern plains and adjacent areas.

In summary, the evolutionary affinities of the Great Plains are most marked with the avifauna of higher latitudes, although a few cases suggest interactions with other areas. Other species of probably Great Plains origin show relationships with South American forms and with other New World forms, although ultimately some of these relationships also go back to the Old World. I cannot account for the evolutionary histories of these largely obscure, southern-related species. With the same evolutionary model, the interaction between the Great Plains and northern latitudes also extends to certain birds of forests and other habitats of the holarctic. The major Great Plains refugium involved in this northern interaction was probably in the Nebraskan Sandhills, as the merging there of grassland and tundra may have been more favorable for arctic birds than areas farther south. On a lesser scale, the Gulf Refugium may also have yielded forms of the Great Plains and vicinity, these being mainly species with more southern relations.

## *Conclusions*

In this study, I have developed models showing how many modern bird species of aridlands and associated areas may have arisen during the Pleistocene, particularly during the last two glacial intervals. Among the endemic, and near-endemic, species of aridlands listed in Table 1, at least three-fourths may have differentiated in the latter half of the Pleistocene. Others have also proposed an equally recent origin of bird species (Rand, 1948; Mengel, 1964 and 1970); but it is noteworthy that so many species from the total avifauna seem to be involved. Such recent origin is not surprising, in view of the rapidity with which changes in morphology are now known to have occurred in such species as the House Sparrow (*Passer domesticus*) in North America (Johnston and Selander, 1964). On the other hand, a relatively recent origin of some modern species does not mean that the ancestors from which they stem evolved recently. For example, modern forms of *Tympanuchus* may be only of Wisconsin age, but the genus goes back to the lower Miocene (Wetmore, 1956). We can expect this generic antiquity among many North American birds, including passerines. It is probable that an aridland avifauna existed in North America by the mid-Pliocene, and it seems likely that certain birds, especially those which seem to lack close relatives, may represent the remnants of that ancient avifauna. These could include *Aechmophorus, Centrocercus, Tympanuchus* (including *Pedieoectes*), *Callipepla* (including *Lophortyx*), *Geococcyx, Auriparus, Oreoscoptes, Xanthocephalus, Spiza,* and *Calamospiza.*

Birds that probably originated in the Southwestern Aridlands (Tables 1 and 2) show a marked tendency toward sedentariness, or are at least limited migrants. Only members of the Nashville Warbler (*Vermivora ruficapilla*) complex are highly migratory, while others such as the Mexican Duck, Costa's Hummingbird, Bendire's Thrasher, Cassin's Sparrow, and probably Worthen's Sparrow are, at most, partially migratory. If one can assume a similar degree of sedentariness during glacial intervals, then we can explain how such a high level of speciation came about in the Southwestern Aridlands and adjacent regions. The low dispersal rate obviously reinforced the separation of isolates in the insular refugia, thus fostering inbreeding of populations and the rapid attainment of differentiation. On the one hand, one finds that species of the Great Plains (Table 1) show greater migratory behavior, which is not unexpected in view of the rigors of winter there. Among the species that probably originated in the Plains, or are endemic there, only the Prairie Falcon and the Greater Prairie Chicken remain there throughout the year, all the others moving south for the winter. Such species as Baird's Sparrow, Lark Bunting, Clay-colored Sparrow, Chestnut-collared Longspur, and McCown's Longspur desert their breeding ranges in the Plains to winter extensively in the Southwestern Aridlands. Furthermore, the winter or migratory ranges of most Great Plains species include one or more of the areas postulated here to have been glacial refugia. Given this degree of dispersal, it is not surprising that such a low degree of evolutionary interaction seems to have involved the Great Plains and other glacial refugia of North America. On the other hand, the differentiation of isolates divided between the Great Plains and Beringia Refugia was probably hampered not at all by any dispersal between them. Not only was the barrier (i.e., glaciers) much more formidable in keeping isolates separated, but it probably also ruled out dispersal through migration as well. As a result, Great Plains isolates probably wintered strictly in the New World, whereas those of Beringia wintered in the Old World.

In this paper I emphasized the positive effect of Pleistocene events on the aridlands avifauna of North America, but the negative effects are also relevant. During glacial intervals, the aridlands of the continent were not only reduced in size and altered in location, but undoubtedly were subjected to invasion by biotic elements from more mesic communities. Thus, disjunction, infiltration, and other alterations confronted aridlands birds, with the net effect that the character of the avifauna may have been markedly changed from its Pliocene aspect. The changes probably caused extinction for some birds, while others adapted and survived. The net result, however, was an avifauna less specialized in its adaptations to aridity and xeric habitats.

Most authors have overlooked the probable severity of impact of the Pleistocene on birds of North American aridlands, including Udvardy (1958). He suggested that it is the recency of aridlands and the adaptation to them by birds that accounts for the seeming paucity of xerophiles among the North American avifauna. In his view, species with partial or imperfect adaptations occupy these aridlands, the birds being merely recent offshoots from arboreal (=forest?) genera and families. As an example, he suggested the thrashers (*Toxostoma*), but since most of these species inhabit arid or semi-arid habitats, the assumption that *Toxostoma* is a forest taxon is not well founded. In my view, the more catholic requirements among many North American birds reflect a compromise by aridlands birds with the severe ecological changes thrust upon them during glacial intervals, rather than a recent or incomplete adaptation to aridlands by arboreal species.

The character of the xeric areas, themselves, must be examined in comparing the North American aridlands biota with those of the rest of the world. The deserts of North America are but a fraction of the size of those of the Old World (Africa, Eurasia, and Australia), and the average severity of climate is probably less. For example, the Sahara Desert dwarfs the North American scrub deserts and, except for such areas as Death Valley, the former is hotter, drier, and less heavily vegetated. The Great Plains, while somewhat smaller than the steppes of Eurasia, is probably more similar to its Old World counterpart than are deserts of the two hemispheres; nevertheless, comparisons must be made judiciously. In deserts, one should expect greater diversity among Old World birds than among the birds of the New World on the basis of relative size of the area alone. Furthermore, the more severely arid and less vegetated Old World deserts may elicit greater specialization among avian xerophiles than among those of the New World. The geographic location and spacing among African and Eurasian deserts could also have favored speciation on a larger scale than would be possible in New World areas. Finally, although the aridlands of the Old World were subjected to ecological trauma of the Pleistocene, this probably was less severe and less widespread on the biota than on that of the New World, if for no other reason than the relative extent of the land area covered by aridlands. Thus, it appears that other factors must be considered in addition to time of origin in assessing any relative diversity and degree of specialization in the aridlands avifauna of North America, as compared with the Old World.

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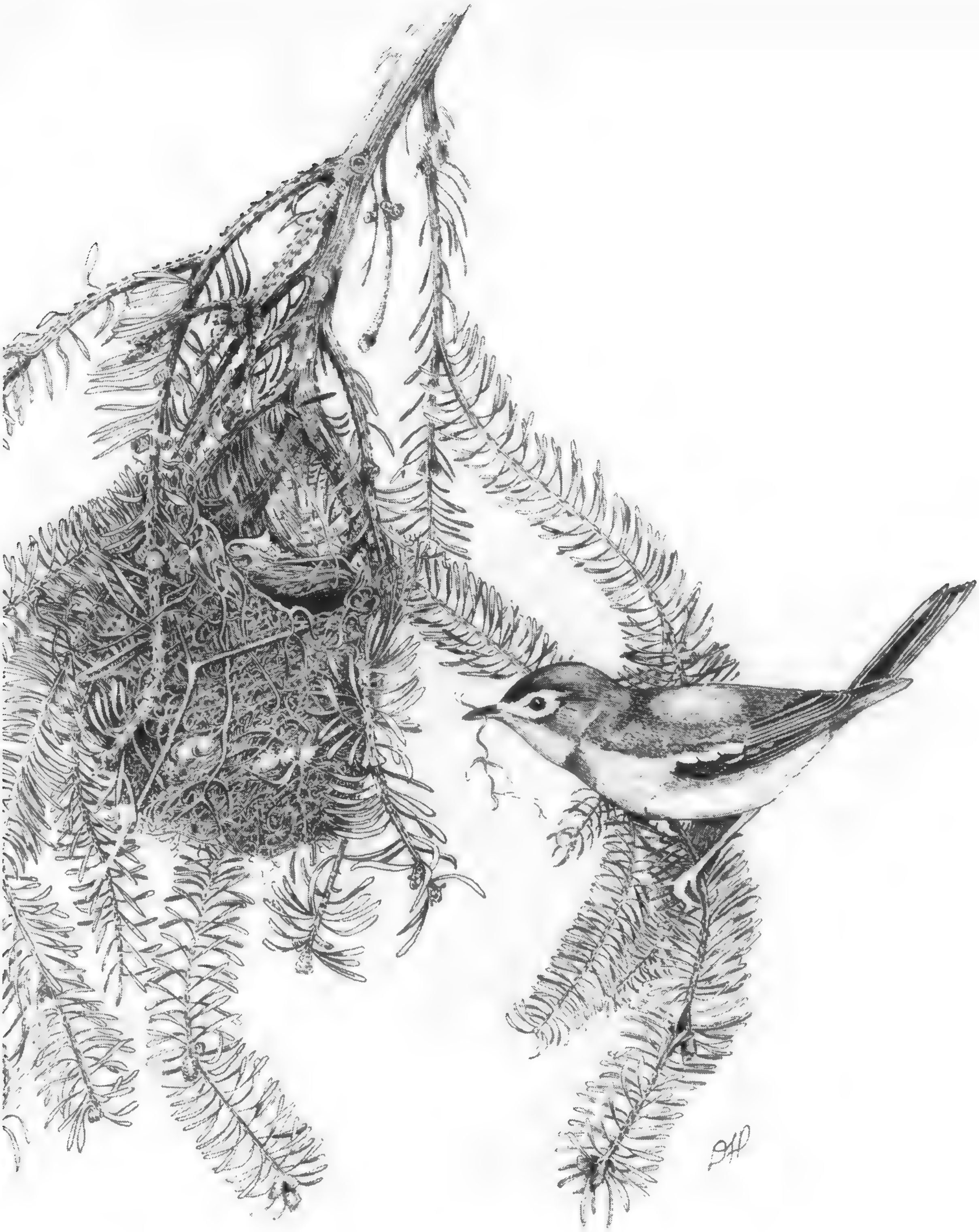
# THE NEST OF THE NORTHERN PARULA

David F. Parmelee

I became familiar with the Northern Parula (*Parula americana*) and its unique nesting habits years ago in the swamps and oak forests of South Carolina. There, without exception, I found the birds nesting in great pendulous masses of grayish Spanish moss (*Tillandsia usneoides*), a common flowering plant of the south found draped on countless tree limbs at varying heights. In northern United States and southern Canada, where there is no wild-growing Spanish moss, the Northern Parulas seek out and nest within heavy strands or festoons of a greenish lichen called "old man's beard" (*Usnea cavernosa*) which, unlike its distantly related southern counterpart, is abundant only in certain areas. In the boreal forests of Itasca State Park, breeding parulas are common, but they have been thought to be confined very locally during nesting, usually within, or at the edges of, black spruce bogs where *Usnea* grows abundantly in some places. In tracking down the Northern Parulas, one usually searches for these special places and then listens carefully for the high notes of the small, arboreal warbler. One seldom fails to find one or more during the proper season.

In 1971, at the University of Minnesota Forestry and Biological Station on the shores of Lake Itasca, several singing males took up residence high in the towering white spruces and balsam firs of the station, despite the fact that *Usnea cavernosa* is not known to occur on the campus. We watched these males for sometime and finally concluded that they were non-breeding individuals that spent their long summer days singing from lofty perches.

In late June that year, I saw a male Blackburnian Warbler (*Dendroica fusca*) disappear into a clump of spruce needles some forty feet above the campus grounds. The bird remained there long enough to warrant investigation by one of the students in a field project on the Blackburnian, which up to that time had failed to reveal a single nest to any of us. There was a nest concealed in the spruce, to be sure, but hardly the one expected. Instead of being saddled on a limb in typical Blackburnian fashion, this nest was a suspended, gourd-shaped structure that looked much like the nest of an oriole, except for its tiny size. Moreover, it was a finely knit structure of *Usnea cavernosa* that must have been brought in from some source far outside the male's territory. Climbing to the nest in early July, I identified its single egg as that of a Northern Parula.



Northern Parula and its nest. Drawing by David F. Parmelee.

Better known nests of Northern Parulas at Itasca State Park and elsewhere are vastly different: the nesting bird punches a hole in a natural mass of *Usnea cavernosa,* shapes a hollow within, and eventually adds the scantiest of linings. In western parts of the species' range, where no *Usnea* or *Tillandsia* grows, Northern Parulas reportedly nest in the lace lichen (*Ramalina reticulata*). Where it, too, is lacking, the birds resort to a variety of other nesting materials and sites. Perhaps the most bizarre nest of the species ever reported was found near Copan, Oklahoma, and was described by Margaret Nice in "The Birds of Oklahoma," (Volume 3, Publication Oklahoma Biological Survey, revised edition, 1931). This nest, supported by a stick and a swaying cluster of ivy leaves, was built ". . . almost entirely of box elder blossoms held together by spider webs on the outside, and sycamore seed down on the inside with a lining of fine strips of weed stems."

A nest apparently quite similar to our Itasca bird's was found by Henry Mousley of Hatley, Quebec, in the mid-twenties. This Northern Parula made its nest entirely of *Usnea,* all brought from a distance, lined it with hair-like rootlets and plant down, and strengthened it with a few, fine grass stems. During a twenty-four period of observation of this nest, the female made 206 trips with nesting material, an average of one load every 5.4 minutes!

The mystery of the nests of Northern Parulas at Itasca Biological Station, which seemingly are very dependent on *Usnea cavernosa,* did not end abruptly with the finding of a nest composed of material brought in from the outside. In looking for the source of the *Usnea,* we learned from a lichen expert, Dr. John W. Thompson of the University of Wisconsin, that none occurred within a mile of the campus. Therefore, the birds carry the lichens a surprisingly long distance. The enigma deepened later when we discovered that Blackburnian Warblers nesting on the campus decorate their cup-like nests on the outside with *Usnea cavernosa.* And, like the Parulas, the Blackburnians evidently shun other species of *Usnea* growing close by. Whether they rob Northern Parula nests of the special lichen or simply carry it in from afar, we have not yet discovered.

The importance of *Usnea cavernosa* in the nest-building techniques of these Itasca warblers is evident. Transporting this vital material great distances, the birds are freed from the confines of an otherwise restricted habitat.

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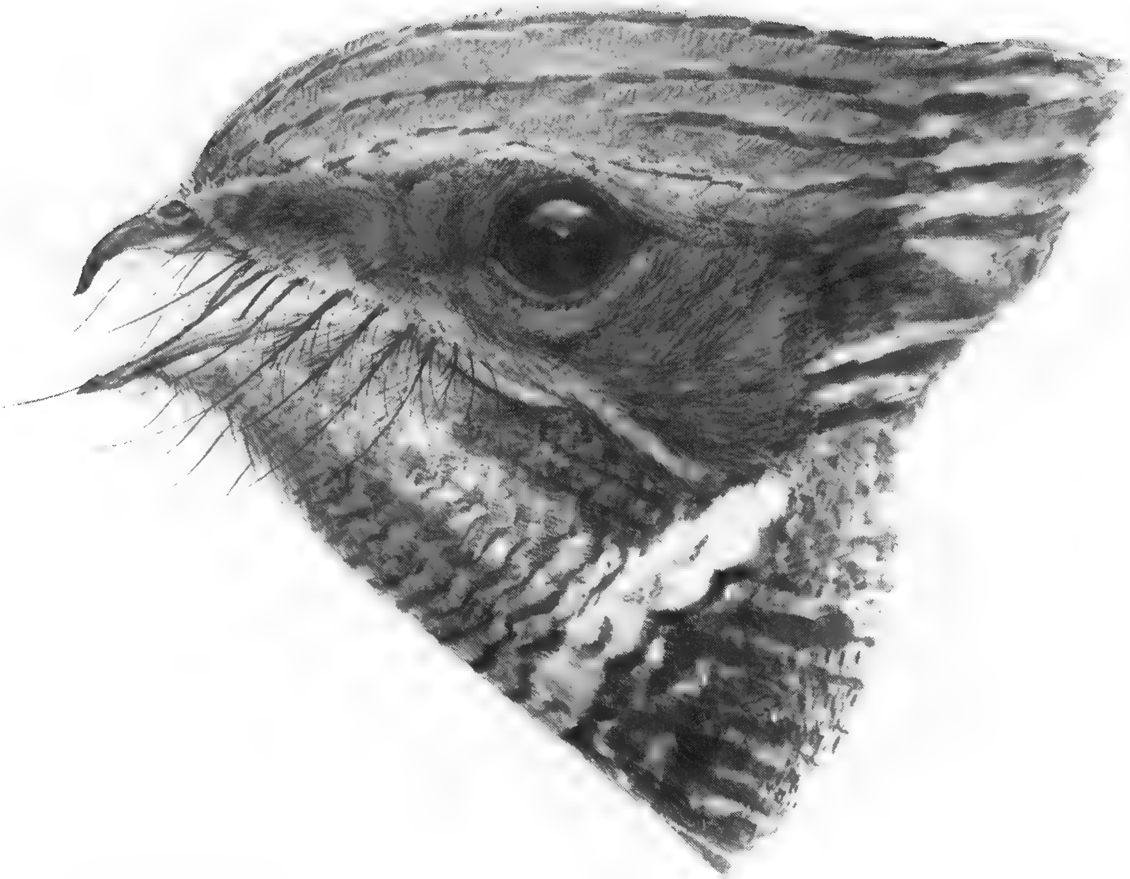

Whip-poor-will, *Caprimulgus vociferus.* Drawing by Louis Agassiz Fuertes.

# THE BRISTLES OF BIRDS

PETER STETTENHEIM

Contour feathers, which cover a bird's body and give it shape, are thought to have evolved from reptilian scales as adaptations for thermal insulation, flight, body covering, and visual effects (Portmann, 1963). Bristles and bristly feathers appear to be structures that have developed from contour feathers for serving other functions. Although bristles are common in birds, they have received little attention. Study might illuminate their roles and indicate their value as taxonomic characters. Many bird books mention the presence of bristles. Lucas and Stettenheim (in press) describe the morphology of certain bristles and bristly feathers, and Küster (1905), Jany (1955), and Lederer (1972) investigated aspects of bristle functions. The present paper will give a preliminary survey of bristles, bristly feathers, and so-called "bristles" in birds, and offer some ideas about their functions.

## *Form and Structure*

Typical avian bristles are feathers with a stiff, tapered rachis and without barbs except at the base (Figure 1). They are sometimes described as hair-like but this is inaccurate because they are stiffer and relatively thicker at the base than hairs. Bristles have been confused with filoplumes, which *are* truly hair-like, but the two kinds of feathers are fundamentally different. As shown in Figure 2, the rachis is tapered and rather stiff in bristles but filamentous and more flexible in filoplumes. Bristles often have barbs at the base, never at the tip. Filoplumes usually have tiny barbs at the tip; they also possess long barbs at the base while they are growing but lose them when fully grown. Bristles grade into contour feathers morphologically and replace contour feathers in the tracts. Filoplumes do not intergrade, and they are always situated beside other feathers. Microscopic sections of the skin show that bristle follicles are operated by feather muscles whereas filoplume follicles are not. Bristles and filoplumes can readily be compared on the head of a male Scarlet Tanager (*Piranga olivacea*), where both types are black and conspicuous against the red background. The bristles are situated above the rictus and in the malar region, while the filoplumes are in the gular region and on top of the head.

The tips of the bristles along the rear border of the upper beak are enlarged or branched or both in at least 12 families of birds (Jany, 1955). Many of these end-bodies bear variously shaped projections which seem to be characteristic for certain families. The end-bodies have been overlooked because of their small size and the fact that they commonly break off from the bristles in museum skins. These structures, like all feather tips, are the first part of the feathers to grow, not the last, as Jany (1955:276) implied.

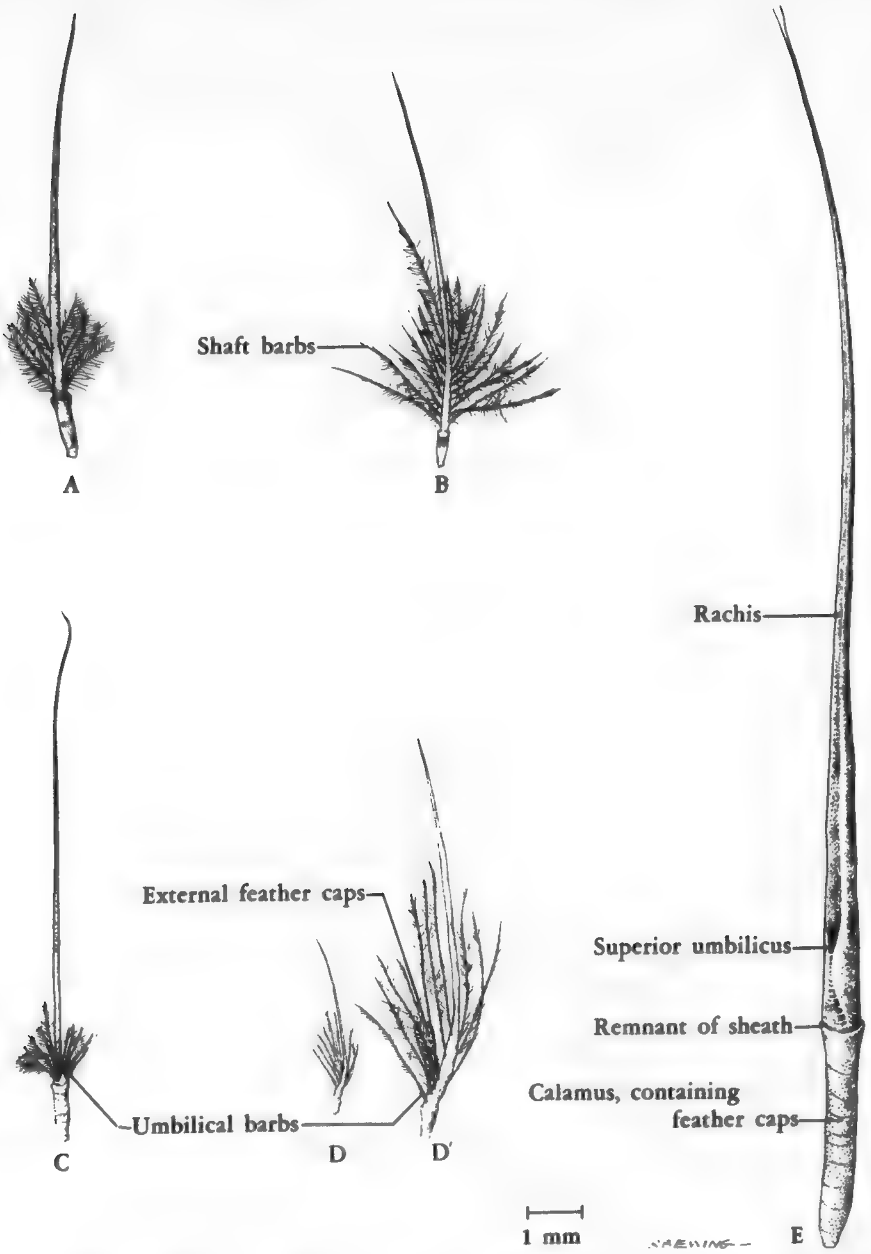

Figure 1. Five typical avian bristles. A. Rictal bristle of Robin, *Turdus migratorius*. B. Rictal bristle of Common Starling, *Sturnus vulgaris*. C. Eyelash of Red-tailed Hawk, *Buteo jamaicensis*. D. Eyelash of Common Starling, *Sturnus vulgaris*. D′. Same as D. but magnified 2.2X to show details. E. Rictal bristle of Band-winged Nightjar, *Caprimulgus longirostris*. From Lucas and Stettenheim, in press by courtesy of U. S. Dept. Agr.

Contour feathers, semiplumes, and down feathers of many birds possess small filamentous or feather-like outgrowths on the underside of the shaft, collectively termed afterfeathers. As part of their simplification, nearly all bristles either lack an afterfeather entirely or have only a tuft of short, umbilical barbs. The bristles on the otherwise naked head of turkeys and certain cathartid vultures are unusual in having a distinct aftershaft. Each of these bristles appears to consist of two shafts, one longer than the other (Figure 3).

The bare portion of the rachis and any barbs, if not the entire bristle, is usually dark brown or black, indicating the presence of much melanin pigment. This is conspicuous in the many cases where adjacent contour feathers and the basal parts of the bristles are pale. Dark coloring, at least on the tips, is indeed the typical condition in bristles. We know from gross observations that dense concentrations of melanin not only darken a contour feather but also make it more resistant to wear and photochemical changes (Rand, 1967: figure 36). Electron microscopic findings support this (Carr, 1957). Likewise, heavy melanization probably increases the stiffness and hardness of bristles. Lightly pigmented or unpigmented bristles are not only unusual but also seem more flexible than dark ones. Such pale bristles occur, for example, on the cere of the White-tailed Kite (*Elanus leucurus*) and the Barn Owl ( *Tyto alba*), and on the chin of the Cuban Tody (*Todus multicolor*).

Aside from melanin, the barbs and the proximal part of the rachis in bristles exhibit other kinds of coloring, usually the same as in adjacent contour feathers. Carotenoid pigments are visible, for example, in bristles of the Yellow-headed Parrot (*Amazona ochrocephala*), Cuban Tody, Yellow-billed Barbet (*Trachyphonus purpuratus*), Scarlet Tanager, and Western Meadowlark (*Sturnella neglecta*). We see blue or blue-green, caused by Tyndall scattering, on bristles of the European Bee-eater (*Merops apiaster*), European Roller (*Coracias garrulus*), Crimson-rumped Toucanet (*Aulacorhynchus haematopygus*), and Piñon Jay (*Gymnorhinus cyanocephala*).

True bristles occur almost exclusively on the head and neck. Barn Owls are unusual in having bristles on the toes; certain other owls and grouse also have bristle-like feathers on the toes. Feathers that resemble bristles in some respects occur on the knee region of the Bristle-thighed Curlew (*Numenius tahitiensis*). Bristles on the head can be found about the base of the bill, on the lores, on the eyelids, around the eyes, on the malar and gular regions, and elsewhere (Figure 4 and 5). Those above the base of the bill and on the lores are sometimes known as "vibrissae." It is often convenient to refer to bristles according to their location — such as rictal, loral, narial, or supraorbital (Chandler, 1914) — but one should ascertain said locations carefully. The term "rictal bristle," for example, properly applies only to bristles above the rictus, not to *all* bristles along the rear edge of the upper beak.

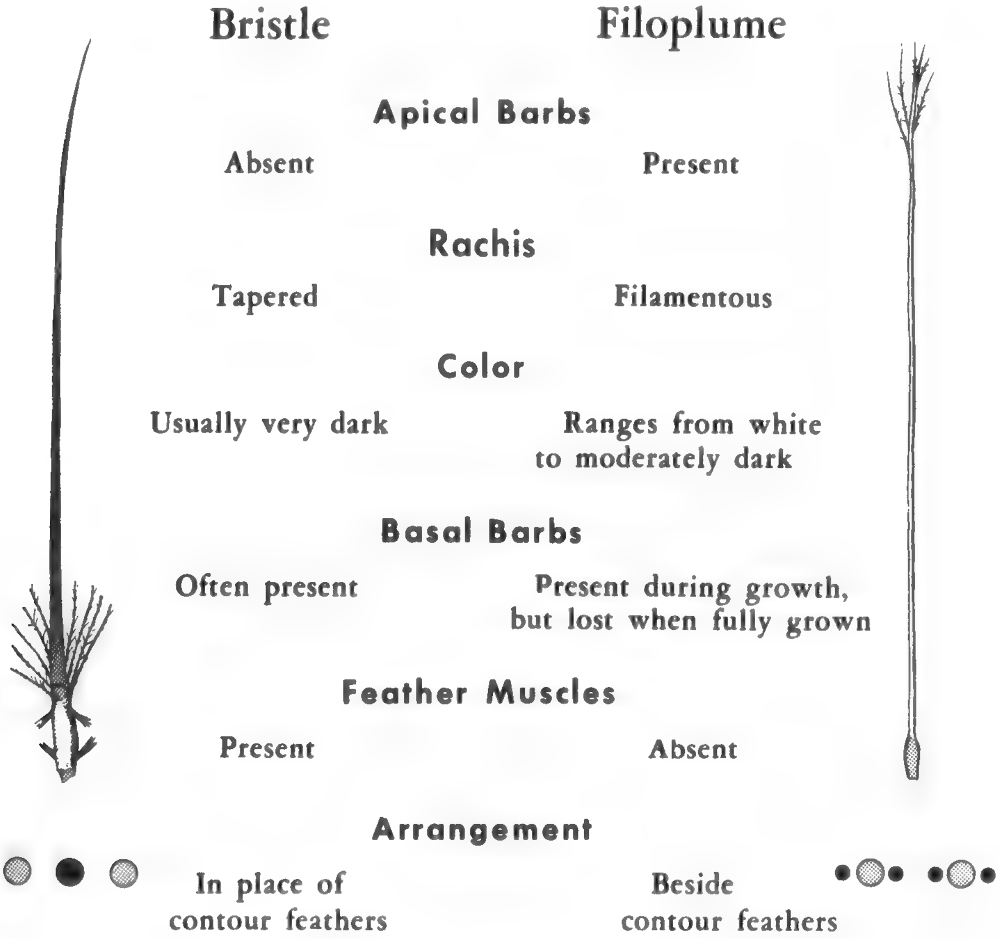
Bristle
Filoplume
Apical Barbs
Absent
Present
Rachis
Tapered
Filamentous
Color
Usually very dark
Ranges from white to moderately dark
Basal Barbs
Often present
Present during growth, but lost when fully grown
Feather Muscles
Present
Absent
Arrangement
In place of contour feathers
Beside contour feathers

Figure 2. Comparison of a typical bristle and a filoplume.

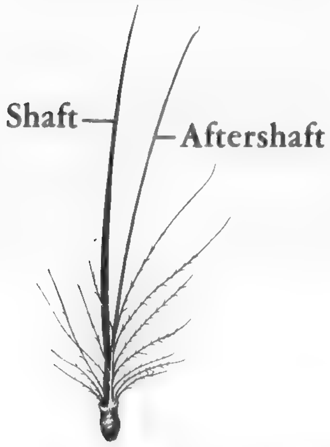

Figure 3. Bristle from malar region of Common Turkey, *Meleagris* gallopavo, showing a long, bare aftershaft as well as a shaft. From Lucas and Stettenheim, in press, by courtesy of U. S. Dept. Agr.

A bristle's location does not automatically tell anything about its structure, and vice versa. Bristles at different locations on a bird's head usually differ in details but they may be very similar (Figure 1-B, D). Conversely, feathers from similar sites in different birds may be very different (Figure 1-A, E). The term "eyelash" is sometimes applied to stout bristles on the eyelids, but I shall use it in a broader sense, referring to any feather on the rim of the eyelids, regardless of structure.

A graded morphological series between ordinary contour feathers and barbless, or bare, bristles can be found in many birds, such as the Marsh Hawk (*Circus cyaneus*), according to Chandler (1914). Lucas and Stettenheim (in press) found it useful to recognize an intermediate form of feathers on this continuum, or gradation, and suggested that it be called "semibristle." Semibristles show various signs of bristliness, but usually the distal portion of the rachis is stiffened and conspicuous, distal barbs are reduced and spread apart,

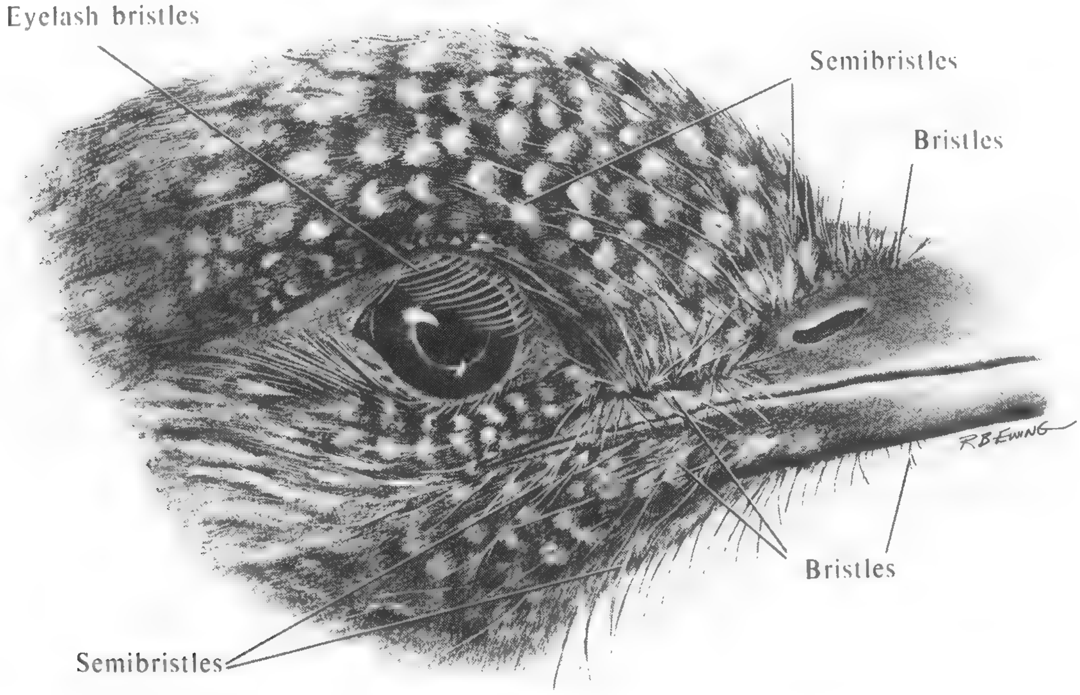

Figure 4. Roadrunner, *Geococcyx californianus*.

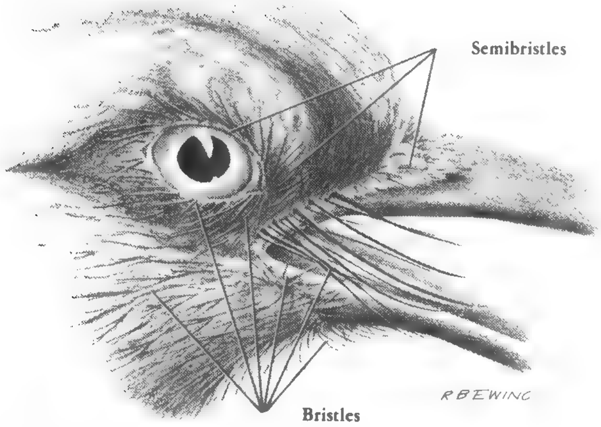

Figure 5. Blue Jay, *Cyanocitta cristata*.

and the barbules are reduced or absent on most of the barbs (Figure 6). Often, one of the first signs of bristle formation in a gradient from contour feathers is the darkening of the tip of the rachis and the distal barbs. In a series of feathers, the proximal portions of the rachis and barbs tend to become darker as they are reduced. In addition to melanin pigmentation, semibristles show the same kinds of color as contour feathers, including iridescence, like that on the lores of the Common Grackle (*Quiscalus quiscula*). Semibristles occur on many birds, with or without bristles, but are especially well developed in hawks, owls, and some caprimulgiforms such as nighthawks. Conversely, bristles are sometimes present without semibristles, as in the Australian Cassowary (*Casuarius casuarius*), cathartid vultures, guineafowl, and certain hornbills.

Bristles and semibristles tend to project outward from the surface of the body instead of conforming to the contours. This might not seem to be an unusual trait in rictal bristles and eyelashes, but it gains significance when it is found to be the prevalent condition elsewhere on the head and neck. One of the first signs noted in a series from contour feathers to semibristles or bristles is that the bare tips of the rachis and apical barbs point outward. Further on, the whole feathers angle outward more, and hence tend to stand apart from each other instead of overlapping closely. One can see this well on many birds by viewing the sides of the head from above (Figure 7).

## *Survey of Birds*

Bristles and semibristles are commoner in birds than we generally suppose. In speaking of these feathers — if they mention them at all — ornithological textbooks usually refer only to the rictal bristles of nightjars and flycatchers — in both New World and Old World groups, the loral semibristles of hawks and owls, and the eyelashes of ostriches, hoatzins, hornbills, and many cuckoos. In order to find out where else bristles occur, I examined fresh and frozen specimens and museum skins representing all 28 orders and 117 of the 156 families of living birds as classified by Storer (1971). Information in the literature amplified these findings and gave answers for five additional families. Altogether, I found bristles or semibristles in representatives of 19 orders and 89 families of birds. I suspect that such feathers are also present in many of the families for which I had no information.

As a result of this survey, I discovered that the ornithological literature is often unreliable as to the presence or absence of bristles. Even descriptions of birds as detailed as those of Ridgway and Friedmann (1901–1950) or Witherby *et al.* (1943) sometimes omitted mention of bristles in birds where I found them present, and sometimes referred to certain structures as bristles that I would not consider as such except under a very loose definition of that term. I suggest that in the future bristle-like feathers be described briefly and not simply referred to by that name.

The following survey of bristles, semibristles, and so-called "bristles" is far from complete, but it is sufficient to show the prevalence of these structures in birds. The list includes only those families for which I had information, either by personal examination or from the literature. The term "none" signifies the apparent absence of bristles or semibristles.

Order Tinamiformes

Family Tinamidae, tinamous

*Tinamus major* (Great Tinamou). — None.

*Rhynchotus rufescens* (Red-winged Tinamou). — Upper and lower eyelashes are dark, barbed bristles.

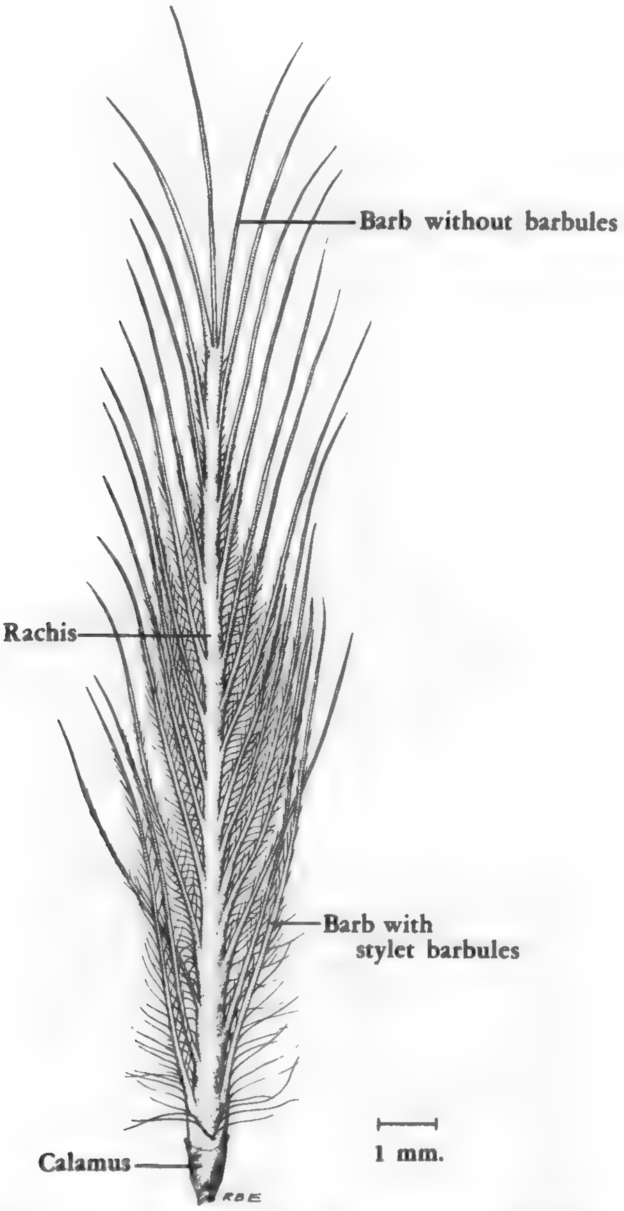

Figure 6. Loral semibristle of Great Horned Owl, *Bubo virginianus*. Lucas and Stettenheim, in press, by courtesy of U. S. Dept. Agr.

Figure 7. Great Horned Owl, *Bubo virginianus*. Bill and front of head viewed from above, showing bristles and semibristles projecting outward from the surface.

Order Rheiformes

Family Rheidae, rheas

*Rhea americana* (Greater Rhea). — Coarse contour feathers on top of head grade anteriorly into semibristles and bristles at base of bill. Bristles are mostly or entirely dark brown, but semibristles are pale and weak. Upper eyelashes are semibristles and lower eyelashes are small dark bristles.

*Pterocnemia pennata* (Lesser Rhea). — Similar, but mostly semibristles with dark rachis and pale barbs (Figure 8).

Order Struthioniformes

Family Struthionidae, Ostrich

*Struthio camelus* (Ostrich). — Thin bristles are the predominant form of feathers on the top and sides of the head; they project outward from nearly bare skin. Bristles are up to 38 millimeters long, the small ones bare and black but the larger ones often with basal barbs and only partly dark or entirely pale. Rows of bare dark bristles on eyelids. Pale bristles and semibristles with bare rami, or branches, densely screen ear opening. Pale thin bristles with basal barbs are sparsely present on the upper portion of the neck, grading downward into semiplumes and contour feathers (Figure 9).

Order Casuariiformes

Family Dromiceidae, emus

*Dromiceus novaehollandiae* (Common Emu). — Many black bristles around eyes, on lores, forehead, and malar region. The longest bristles, up to 32 mm, point forward from the forehead. Most bristles have short basal barbs but some are bare. Black semibristles behind eye and around ear opening.

Family Casuariidae, cassowaries

*Casuarius casuarius* (Australian Cassowary). — Many black bristles, most of them bare, around the eyes and rictus, and on the lores up to the base of the casque. Small feeble bristles on malar region, chin, below eye, and on neck. Dark semibristles and coarse contour feathers on the body.

Order Dinornithiformes

Family Apterygidae, kiwis

*Apteryx australis* (Brown Kiwi). — Many dark brown bristles project in various directions around the rictus, on the lores, forehead, and gular region. A few forehead bristles extend nearly to the tip of the beak; as much as 120 mm long, they are the longest bristles known in birds (Figure 10). These grade posteriorly, toward the back, into semibristles and coarse contour feathers. Many thin, bare eyelash bristles. Bristles and semibristles also radiate from an area below each eye. The bristles have a flat, all-dark rachis, the longer ones being darker; barbs, where present, are relatively short and pale.

Order Podicipediformes

Family Podicipedidae, grebes

*Poliocephalus poliocephalus* (Hoary-headed Grebe), *Colymbus auritus* (Horned Grebe), *Podiceps major* (Great Grebe). — None.

*Podilymbus podiceps* (Pied-billed Grebe). — Feathers on the lores, forehead, and malar region can be considered semibristles. The rachis is broad, flattened, but curved at the edges, conspicuous, and barbless for at least the distal half of its length (Figure 11). Minute projections at the tips of some feathers probably represent rudiments of barbs fused into the rachis. These feather tips thus combine features of both the waxwing and rail and the cuckoo and araçari types of feather tips (Brush, 1967). The feathers are as much as 7 mm long, and they bear as many as six pairs of barbs at the base; tips of the barbs lack barbules, the projections from rami. The bare portion of the rachis is dark brown proximally but pale or unpigmented at its tip. The feathers project backward, conforming to the contour of the head. The Atitlan Grebe (*Podilymbus gigas*) has feathers similar to these (R. W. Storer, pers. commun.).

Order Sphenisciformes

Family Spheniscidae, penguins

*Aptenodytes patagonicus* (King Penguin), *Pygoscelis adeliae* (Adélie Penguin), *Eudyptes chrysolophus* (Macaroni Penguin). — None.

*Spheniscus magellanicus* (Magellanic Penguin). — Several rows of bristles on the lores and the base of the upper and lower bill, on the transition between the rhamphotheca, or horny sheath of the bill, and the feathered skin (Figure 12). The bristles are as much as 1.5 mm long, and they grade into contour feathers; some of the dark brown bristles have a few barbs but the rest, both dark and pale, are bare.

*Spheniscus mendiculus* (Galapagos Penguin). — None.

Order Procellariiformes

Family Diomedeidae, albatrosses

*Diomedea exulans* (Wandering Albatross). — None.

Family Procellariidae, petrels and shearwaters

*Macronectes giganteus* (Giant Fulmar), *Pterodroma inexpectata* (Mottled Petrel), *Puffinus pacificus* (Wedge-tailed Shearwater). — None.

Family Hydrobatidae, storm-petrels

*Oceanodroma leucorhoa* (Leach's Storm-petrel). — None.

Family Pelecanoididae, diving-petrels

*Pelecanoides garnotii* (Peruvian Diving-petrel). — None.

Order Pelecaniformes

Family Phaethontidae, tropicbirds

*Phaethon rubricauda* (Red-tailed Tropicbird), *P. lepturus* (White-tailed Tropicbird). — None.

Family Sulidae, boobies and gannets

*Morus capensis* (Cape Gannet), *Sula bassana* (Northern Gannet). — None.

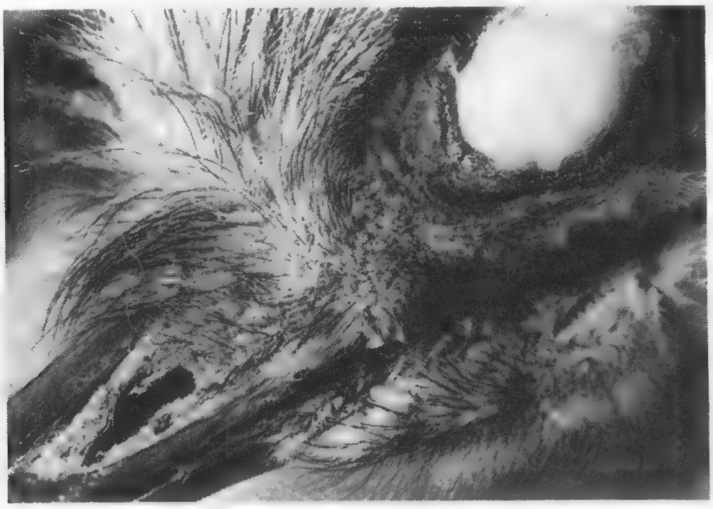

Figure 8. Lesser Rhea, *Pterocnemia pennata*. Bristles and semibristles at base of bill.

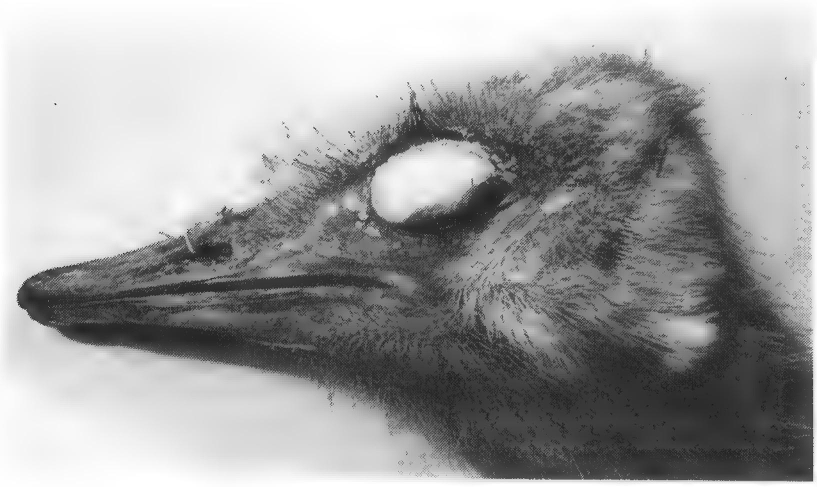

Figure 9. Ostrich, *Struthio camelus.* Bristles on head and upper end of neck.

Family Phalacrocoracidae, cormorants

*Phalacrocorax carbo* (Great Cormorant). — None.

Family Anhingidae, snakebirds

*Anhinga anhinga* (Anhinga). — None.

Family Pelecanidae, pelicans

*Pelecanus rufescens* (Pink-backed Pelican). — None.

Order Anseriformes

Family Anhimidae, screamers

*Anhima cornuta* (Horned Screamer), *Chauna chavaria* (Northern Screamer). — None.

Family Anatidae, swans, geese, and ducks

*Anas platyrhynchos* (Mallard), *Aythya marila* (Greater Scaup), *Bucephala clangula* (Common Goldeneye), *Somateria mollissima* (Common Eider), *Melanitta fusca* (Velvet Scoter), *Mergus merganser* (Common Merganser), *Oxyura jamaicensis* (Ruddy Duck). — None.

Order Phoenicopteriformes

Family Phoenicopteridae, flamingos

*Phoenicopterus ruber* (American Flamingo), *Phoenicoparrus andinus* (Andean Flamingo). — None.

Order Ciconiiformes

Family Ardeidae, herons, bitterns, boatbill

*Ardea herodias* (Great Blue Heron), *Butorides striatus* (Striated Heron), *Nycticorax nycticorax* (Black-crowned Night-heron). — None.

Family Threskiornithidae, ibises, spoonbills

*Theristicus caudatus* (Buff-necked Ibis), *Phimosus infuscatus* (Bare-faced Ibis), *Eudocimus albus* (White Ibis). — None.

Family Ciconiidae, storks

*Mycteria americana* (American Wood Stork), *Jabiru mycteria* (Jabiru). — None.

Order Falconiformes

Family Cathartidae, New World vultures

*Cathartes aura* (Turkey Vulture). — Small black bristles sparsely present on head.

*Coragyps atratus* (Black Vulture). — Black bristles sparsely present over most of head and denser in patches below and behind eyes; some have aftershafts and basal barbs.

*Sarcoramphus papa* (King Vulture). — Black bristles all over head and upper neck, densely set in bands and patches, and sparsely set over larger areas; bristles present as eyelashes and on caruncle below ear opening. Some bristles have a long aftershaft and may have basal barbs.

*Vultur gryphus* (Andean Condor). — Black bristles are sparsely present on the head and upper part of the neck.

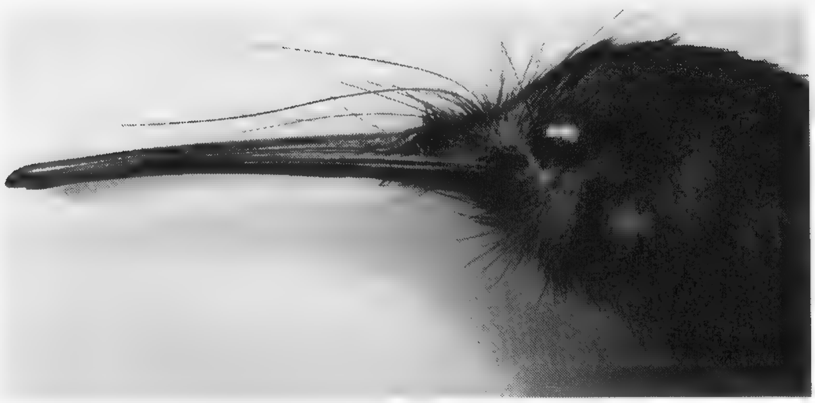

Figure 10. Brown Kiwi, *Apteryx australis*. Long bristles on front of head.

Family Pandionidae, Osprey

*Pandion haliaetus* (Osprey). — Many fine, black bristles on lores, forehead, around rictus, as eyelashes, and on the malar and anterior gular regions. Some bristles are bare, others have a few barbs. Bristles project outward in many directions and grade into contour feathers.

Family Accipitridae, kites, hawks, eagles, Old World vultures. — Most species bear diverging bristles on the lores (Mayaud, 1950).

*Elanus leucurus* (White-tailed Kite). — Black bristles, above eyes as eyelashes and on lores, grade anteriorly into flexible white bristles that project forward over the cere.

*Neophron percnopterus* (Egyptian Vulture). — A few bristles on the head (Witherby *et al.*, 1943).

*Gypaetus barbatus* (Bearded Vulture). — Feathers reduced to a rachis with a few barbs without barbules, or with barbules only on the basal barbs, on the lores, around the base of the bill, and beneath the chin (Mayaud, 1950).

*Circus cyaneus* (Marsh Hawk). — Many thin dark bristles around eyes, on lores, and on the cere, where they curve forward and upward on the sides of the beak. Also on malar and anterior gular regions. Bristles measure up to 10 mm long, and many have basal barbs. See Chandler (1914) for details.

*Accipiter gentilis* (Goshawk). — Black-tipped bristles with basal barbs radiate from the lores, partly covering the nostrils (Figure 13). They grade upward into semibristles and contour feathers.

*Buteo jamaicensis* (Red-tailed Hawk). — Stiff, bare, dark brown bristles up to 14 mm long on the cere and lores. Eyelash bristles with umbilical barbs (Figure 1 C).

Family Sagittariidae, Secretarybird

*Sagittarius serpentarius* (Secretarybird). — Large, very strong, bare eyelash bristles, 30 on the upper lid and 15 below (Nitzsch and Burmeister, 1867).

Family Falconidae, falcons, caracaras.—Caracaras have strongly developed eyelashes (Nitzsch and Burmeister, 1867).

*Falco femoralis* (Aplomado Falcon). — Bristles with basal barbs on lores and as eyelashes. Semibristles with dark-tipped rachis on chin.

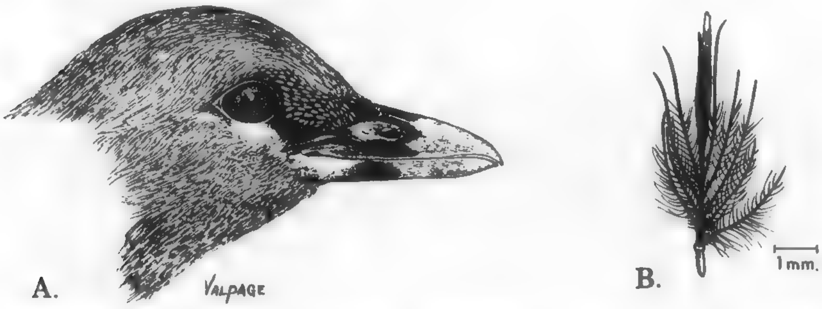

Figure 11. Pied billed Grebe, *Podilymbus podiceps*. A. Slide view of head showing semibristles on lores, forehead, and malar region. B. Loral semibristle.

Order Galliformes

Family Cracidae, curassows, guans, chachalacas

*Ortalis vetula* (Plain Chachalaca). — Stout, bare black bristles on lores grade upward into semibristles and contour feathers; similar bristles around eyes and above rictus (Figure 14). Black barbed bristles in a median row on the chin grade backward into semibristles.

*Penelope superciliaris* (Rusty-margined Guan). — Bare black bristles around eyes, on lores, and behind nostrils; barbed bristles and semibristles on malar region and chin, and widely spaced on bright skin on underside of neck.

Family Opisthocomidae, Hoatzin

*Opisthocomus hoazin* (Hoatzin). — Stout bare bristles, up to 14 mm long, and semibristles around eyes, on lores, and in ear region.

Family Numididae, guineafowl

*Numida meleagris* (Tufted Guineafowl). — Bare black bristles above and below eyes, and on bare skin on the back of the head up to the edge of the casque. Bristles on neck acquire barbs and grade into contour feathers at the lower end of the neck.

*Acryllium vulturinum* (Vulturine Guineafowl). — Stout bare black bristle eyelashes; fine black bristles on bare skin on sides and underside of head.

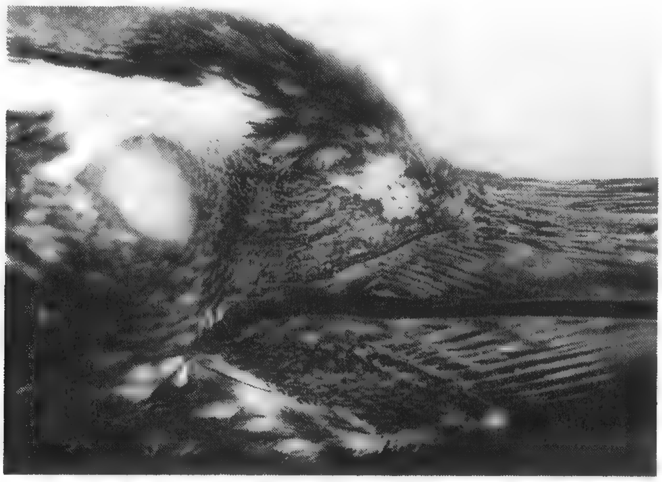

Figure 12. Magellanic Penguin, *Spheniscus magellanicus*. Tiny bristles on lores and base of upper and lower bill, arranged in line with oblique grooves on the rhamphotheca.

Family Phasianidae, grouse, quail, pheasants, turkeys

*Tetrao urogallus* (Capercaillie). — Base of toes "covered by bristly feathers" (Witherby *et al.*, 1943).

*Lagopus lagopus* (Willow Ptarmigan). — White contour feathers on toes grade distally into bristle-like feathers on which basal barbs are reduced and the distal part of the rachis is bare. Lateral projections on the bare rachis indicate the former presence of barbs that have worn off; hence these feathers are not true bristles. The toe feathers of *Tetrao urogallus* are probably similar.

*Bonasa umbellus* (Ruffed Grouse), *Dendrortyx macroura* (Long-tailed Wood-Partridge). — None.

*Lophortyx californicus* (California Quail). — Tiny bare black eyelash bristles. Semibristles with stiff black rachis and pale barbs on lores, forehead, and operculum, grading posteriorly into contour feathers.

*Alectoris chukar* (Chukar Partridge). — None.

*Coturnix coturnix* (Common Quail). — Tiny bare black eyelash bristles on both eyelids (Lucas and Stettenheim, in press).

*Gallus gallus* var. *domesticus* (Domestic Fowl). — Tiny bare white eyelash bristles on both eyelids in Single Comb White Leghorn chickens (Lucas and Stettenheim, in press).

*Phasianus colchicus* (Ring-necked Pheasant). — Tiny bare black eyelash bristles; bristles up to 3 mm long, some bare and others with a tiny basal tuft of barbs, on the caruncles around the eyes and on the lores.

*Meleagris gallopavo* (Common Turkey). — Black bristles and semibristles, many with a long aftershaft (Figure 3), on the exposed, largely caruncular skin of the head and neck, includ-

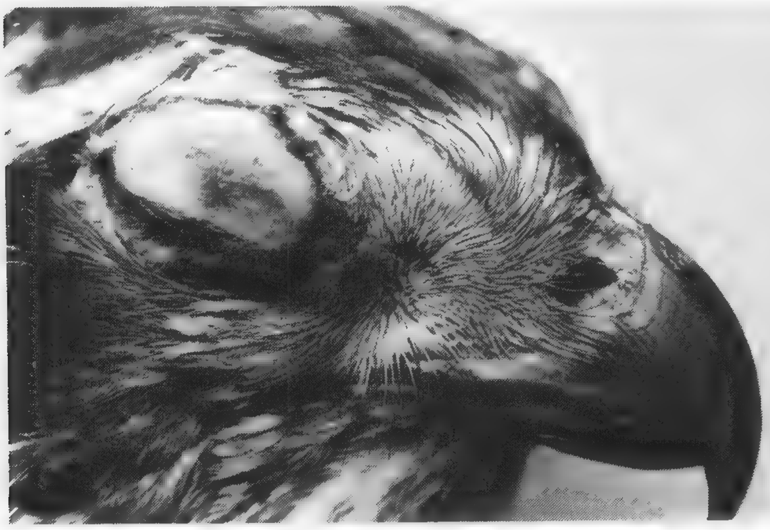

Figure 13. Goshawk, *Accipiter gentilis*. Loral bristles and semibristles.

ing the snood, described in detail and illustrated by Lucas and Stettenheim (in press). The presence of basal barbs and a tapered shaft shows that these feathers are not filoplumes, as thought by Schorger (1966). In an exceptional adult female, "the typical hairlike bristles of the head were accompanied by other feathers with much more vane" (Williams, 1972).

The midventral surface of the lower part of the neck of male and occasionally female turkeys bears a coarse tuft of long, stiff black fibers, commonly called a beard. Búlliard (1926), Lucas and Stettenheim (in press), and Schorger (1957, 1966) described the occurrence, growth, and morphology of this structure. Although the fibers have been called bristles, this is true only in a loose sense of that term. Boas (1931: 580) pointed out that they are totally unlike most bristles of birds, which are modified feathers. The fibers are not seated in follicles but arise close together from the surface of a skin tuberosity, a swelling, known as the beard papilla. They are epidermal filaments with a thick horny layer for most of their length; each has a core of dermal pulp which leaves horny caps as it atrophies. Beard fibers may have a structural affinity to feathers (Lucas and Stettenheim, in press), but they differ from feathers in so many ways that they do not seem to be primitive feathers, as suggested by Schorger.

*Agriocharis ocellata* (Ocellated Turkey). — Bristles on the head are similar to, but smaller than those of the preceding species. There is no beard.

Order Gruiformes

Family Rallidae, rails, coots

*Rallus longirostris* (Clapper Rail), *R. aquaticus* (Water Rail), *R. elegans* (King Rail).— None. Frontal feathers have a more or less accentuated tip of the rachis, owing to prolongation of the rachis beyond the vanes, absence of barbs along the tip of the rachis, broadening, and darkening the tip of the rachis (Brush, 1967). These feathers resemble those described for the Pied-billed Grebe (*Podilymbus podiceps*) but are less modified. They are modified contour feathers, not altered enough to be considered even semibristles.

*Rallus limicola* (Virginia Rail). — None. Frontal feathers not modified.

*Crex crex* (Corncrake). — Bristles in a patch on the side of the operculum project upward and outward. The bristles are up to 2.3 mm long, pale, and have a flat rachis that is wide at the base and bears one or two pairs of barbs.

*Porzana carolina* (Sora), *Fulica americana* (American Coot). — None.

Family Heliornithidae, sungrebes

*Heliornis fulica* (Sungrebe). — None.

Family Eurypygidae, Sunbittern

*Eurypyga major* (Sunbittern). — None.

Family Gruidae, cranes

*Grus grus* (Common Crane). — "Lores, forehead and crown thinly covered . . . with black bristle-like plumes" (Witherby *et al.*, 1943).

*Grus canadensis* (Sandhill Crane). — Fine brown bristles thinly cover the warty skin of the lores, forehead, crown, and around the eyes. The bristles are up to 6 mm long, have only one or two tiny umbilical barbs, if any, and curve posteriorly, close to the surface. They give way to contour feathers on the occiput and do not grade into them.

*Anthropoides virgo* (Demoiselle Crane). — None.

*Balearica pavonina, B. regulorum* (Crowned Cranes). — Many stiff, strawlike bristles in a cluster on the occiput, radiating from a small spot (Walkinshaw, 1964). The bristles are as much as 105 mm long, and the rachis is flattened and uniquely twisted as many as 12 times along its length (Figure 15). Rami without barbules are spaced at wide intervals all the way to the tip, where there is a tiny tuft of them. Some bristles are pale on both sides whereas others are dark on one side and white or pale yellow-brown on the other (L. H. Walkinshaw, pers. commun.). Owing to the twisted rachis, these latter bristles appear to have alternating pale and dark bands (Hesse, 1907). Most bristles have a black tip.

Family Aramidae, Limpkin

*Aramus guarauna* (Limpkin). — None.

Family Psophiidae, trumpeters

*Psophia crepitans* (Gray-winged Trumpeter). — None.

Family Cariamidae, seriemas

*Chunga burmeisteri* (Black-legged Seriema). — Stout, bare, black eyelash bristles up to 16 mm long on upper eyelids. Semibristles up to 25 mm long, with black rachis and white barbs, widespread on head (Figure 16).

Family Otididae, bustards. — "Some with long bristly feathers on sides of head or neck" (Van Tyne and Berger, 1959). As shown in a drawing of a male Great Bustard (*Otis tarda*. Witherby *et al.*, 1943), these appear to be long, coarse contour feathers.

Order Charadriiformes

Family Jacanidae, jacanas

*Hydrophasianus chirurgus* (Pheasant-tailed Jacana). — None.

Family Haematopodidae, oystercatchers

*Haematopus ostralegus* (European Oystercatcher). — None.

Family Glareolidae, pratincoles, coursers

*Rhinoptilus chalcopterus* (Violet-tipped Courser). — Feathers in front of and below the eyes can be considered semibristles because they have a black rachis that is prolonged and bare beyond the basal vanes. Feathers are up to 14 mm long, the longest being below the eyes. The rachis is thin and flexible, but the barbules on the rachis make it more conspicuous.

Family Charadriidae, plovers, lapwings

*Vanellus chilensis* (Southern Lapwing). — Bristles project upward and backward in front of and below the eyes. The bristles, up to 6 mm long, have a broad black shaft and white basal barbs.

*Vanellus crassirostris* (Long-toed Lapwing), *V. indicus* (Red-wattled Lapwing).—None.

*Pluvialis squatarola* (Black-bellied Plover), *P. dominica* (American Golden Plover). — Contour feathers in front of and below the eyes have bare, dark brown tips to the barbs.

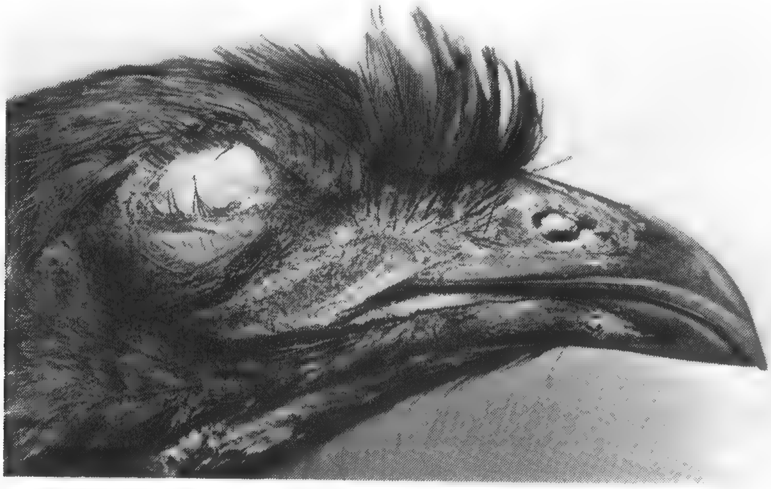

Figure 14. Plain Chachalaca, *Ortalis vetula*. Loral bristles and semibristles, bristles around eyes and above rictus.

*Pluvialis apricaria* (Eurasian Golden Plover). — Tawny feathers in front of and below the eyes and on the lores are smaller than those in the preceding species and can be considered semibristles. The rachis, as well as the apical barbs, is bare and black on its distal one-third, and the tips of the barbs are spread apart.

*Charadrius hiaticula* (Ringed Plover). — Similar to above.

Family Scolopacidae, woodcocks, snipes, sandpipers, turnstones, phalaropes, etc.

*Numenius phaeopus* (Whimbrel), *N. arquata* (Eurasian Curlew). — In front of the eyes is a patch of bristles and semibristles with a dark brown rachis and a few long, light brown basal barbs (Figure 17). These grade anteriorly into contour feathers with a bare brown tip to the rachis. Below the eye they grade into semibristles.

*Numenius tahitiensis* (Bristle-thighed Curlew). — As above. This species is known for the so-called "bristles" that arise from the knee region and hang down in front of and outside the legs (Figure 18). The feathers are up to 66 mm long and have pennaceous vanes for up to 25 mm along the proximal portion of the rachis. The vanes resemble those of adjacent contour feathers, being just as large. The remainder of the rachis is bare. On some feathers, nodules on the sides of the bare rachis for part of its length suggest the former presence of barbs, since lost. The exposed portion of the vanes is pale buffy or white, but the rachis is glistening and unpigmented. The rachis does not seem to be stiffened beyond that of a contour feather. These feathers resemble typical bristles only in that the distal portion of the rachis is bare. They differ in having unreduced barbs proximally and in their slender, flexible, unpigmented distal rachis. They are also exceptional in not being situated on the head. I suggest that we regard them as contour feathers with a prolonged rachis, or at least as atypical bristles.

*Arenaria interpres* (Ruddy Turnstone). — Contour feathers in front of and below the eyes have barbs with bare, dark brown tips.

*Phalaropus fulicarius* (Red Phalarope). — Similar to preceding species except that terminal barbules are reduced, not absent, and only apical barbs are affected.

*Scolopax rusticola* (European Woodcock), *Philohela minor* (American Woodcock). — Contour feathers in front of the eyes and on the lores have black, more or less bare, tips to the barbs. Below the eyes, these grade into bristles up to 10 mm long, on which the distal part of the

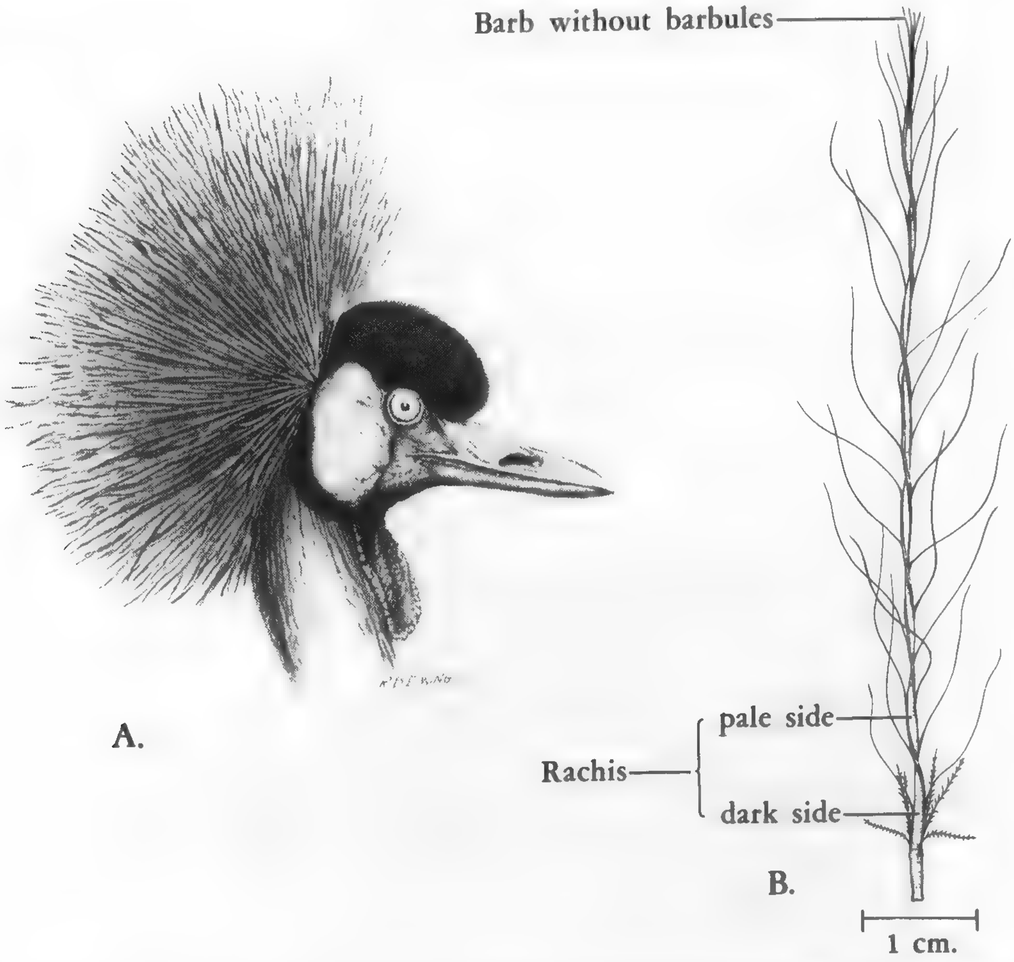

Figure 15. Crowned Crane, *Balearica regulorum*. A. Slice view of head showing cluster of bristles on the occiput. B. Bristle.

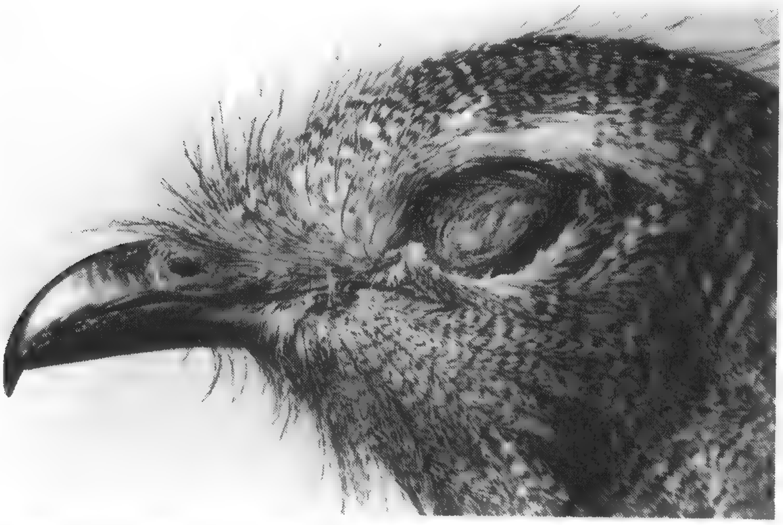

Figure 16. Black-legged Seriema, *Chunga burmeisteri.* Bristles on upper eyelid and semibristles widespread on head.

rachis is stiff, bare, and black, and with small brown or white basal barbs. Posteriorly below the eyes are semibristles up to 12 mm long with bare black tips to the rachis and apical barbs. These feathers project backward, and their black parts stand out against the tawny vanes.

*Aphriza virgata* (Surfbird). — Contour feathers in front of and below the eyes have barbs with bare, dark brown tips.

*Calidris alba* (Sanderling). — Contour feathers in front of the eyes have black, bare tips to apical barbs. These feathers grade ventrally into bristles on which the distal two-thirds of the rachis is stiff, bare, and black, and the basal barbs and rachis are white. Semibristles with black bare tip to rachis and apical barbs below the eyes.

Family Thinocoridae, seedsnipes

*Thinocorus orbignyianus* (Gray-breasted Seedsnipe). — Bristles up to eight mm long project posteriorly and outward on the lores and in front of and below the eyes. The bristles are densest just in front of the eyes, and longest below them. Each bristle has a black rachis, several pairs of reduced basal barbs, and an umbilical tuft.

Family Pteroclididae, sandgrouse

*Pterocles coronatus* (Coronetted Sandgrouse), *P. decoratus* (Black-faced Sandgrouse). — Bristles project backward close against the contour feathers on the operculum, lores, forehead, around the eyes, and the malar and gular regions. The bare portion of the rachis is dark on most bristles but pale on a few. The bristles have a few white or pale basal barbs. Bristles below the eyes are more conspicuous in *decoratus* than in *coronatus* because they are larger, up to 8 mm long, and the bases of the apical barbs, as well as the exposed rachis, are dark.

Family Stercorariidae, skuas, jaegers

*Stercorarius parasiticus* (Parasitic Jaeger). — Bristles project backward on lores and around half of eyes; they are up to 10 mm long with a black rachis and brown barbs.

Family Laridae, gulls, terns

*Larus delawarensis* (Ring-billed Gull), *L. argentatus* (Herring Gull). — In adults, contour feathers below and in front of the eyes have bare tips on the barbs and rachis; feathers are entirely white. In immature birds, where these feathers are gray-brown, the tip of the rachis is bare and dark brown.

*Larus marinus* (Great Black-backed Gull). — Bristles on immature birds are like those of *L. argentatus* but much more conspicuous (Figure 19). Contour feathers on the lores grade posteriorly into semibristles and then bristles close to the eyes. The bristles have a stiff, dark rachis, a few pale basal barbs, and vestigial barbules on the barbs and the rachis. The bristles and the curved tips of the semibristles project outward from the surface in various directions.

*Larus hyperboreus* (Glaucous Gull). — A specimen in prejuvenal molt possesses bristles and semibristles like those described above.

*Sterna hirundo* (Common Tern). — Contour feathers in front of and below the eyes have bare tips to the rachis and barbs.

*Sterna dougallii* (Roseate Tern). — Contour feathers in front of the eye have bare-tipped barbs.

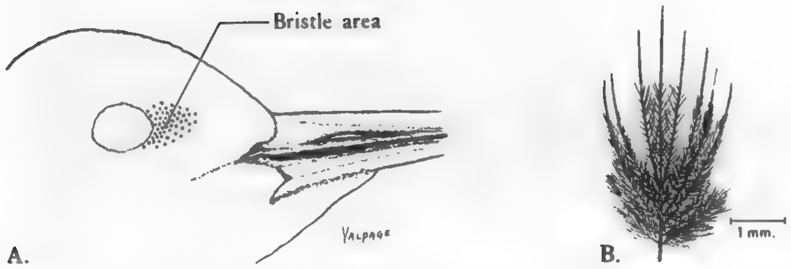

Figure 17. Eurasian Curlew, *Numenius arquata.* A. Side view of head; bristles and semibristles are located in the stippled area in front of the eye. B. Semibristles.

Family Rynchopidae, skimmers

*Rynchops nigra* (Black Skimmer). — Bristles and semibristles in front of and below the eyes; they are either black or white, conforming with adjacent contour feathers. All project outward at their tips, especially the black bristles in front of the eyes.

Family Alcidae, auks, murres, puffins

*Alca torda* (Razorbill). — Bristles project backward and outward below and in front of the eyes. The bristles are 3 to 5 mm long, black, and have a tapered rachis, a few basal barbs, and vestigial barbules.

*Uria lomvia* (Thick-billed Murre). — Similar to preceding species, but bristles are up to at least 7 mm long, stouter, and have more barbs (Figure 20).

*Cepphus grylle* (Black Guillemot). — None.

*Brachyramphus marmoratus* (Marbled Murrelet). — Dark brown barbed bristles in a patch in front of eyes; semibristles below eyes.

*Ptychoramphus aleuticus* (Cassin's Auklet). — As in preceding species, but no semibristles below eyes.

*Fratercula arctica* (Common Puffin). — White semibristles in front of the eyes.

Order Gaviiformes

Family Gaviidae, loons

*Gavia immer* (Common Loon). — None.

Order Columbiformes

Family Columbidae, pigeons, doves

*Columba livia* (Rock Dove), *C. picazuro* (Picazuro Pigeon), *Zenaidura macroura* (Mourning Dove), *Starnoenas cyanocephala* (Blue-headed Quail-Dove). — None.

Order Psittaciformes

Family Psittacidae, parrots, lories

*Ara militaris* (Military Macaw), *Aratinga wagleri* (Scarlet-fronted Parakeet), *A. canicularis* (Orange-fronted Parakeet). — None.

*Pionus seniloides* (White-capped Parrot). — Black semibristles and bare bristles around eyes, on lores, and on cere.

*Amazona pretrei* (Red-spectacled Parrot). — Bare black bristles around eyes.

*Amazona ochrocephala* (Yellow-headed Parrot). — Yellow bristles on the cere, about 2 mm long, with basal and umbilical barbs.

*Amazona versicolor* (St. Lucian Parrot). — Black bristles around eyes, in front of eyes, and on the cere, where they project forward; some are bare, others have a few basal barbs.

Order Cuculiformes

Family Cuculidae, cuckoos. — "Bare colored skin and/or conspicuous eyelashes in many species" (Van Tyne and Berger, 1959).

*Coccyzus erythropthalmus* (Black-billed Cuckoo). — Bare eyelash bristles on bare skin around eyes.

*Coccyzus americanus* (Yellow-billed Cuckoo). — Black semibristles on upper eyelids are about four mm long, with four or five pairs of long barbs; barbules confined to basal portions.

*Coccyzus minor* (Mangrove Cuckoo). — None.

*Piaya cayana* (Squirrel Cuckoo). — Stout dark bristles in rows above and below eyes. Semibristles on operculum and forehead.

*Phaenicophaeus pyrrhocephalus* (Red-faced Malkoha). — Stout, dark, bare eyelash bristles. The superciliary crests are formed by stiff contour feathers in which the distal rami are bare and enlarged for most of their length.

*Dasylophus superciliosus* (Rough-crested Cuckoo), *Lepidogrammus cumingi* (Scale-feathered Cuckoo). — Long eyelash bristles (Mayaud, 1950).

*Crotophaga major* (Greater Ani), *C. sulcirostris* (Groove-billed Ani). — Stout, bare, black eyelash bristles. Semibristles above eyes and on forehead.

*Geococcyx californianus* (Roadrunner). — Stout, bare, black eyelash bristles project outward and backward over eyes (Figure 4). Barbed bristles around the base of the beak grade into semibristles on the forehead and malar region.

*Neomorphus geoffroyi* (Rufous-vented Ground-Cuckoo). — Dark, bare eyelash bristles. Semibristles in front of the eyes.

Order Strigiformes

Family Tytonidae, barn owls

*Tyto alba* (Barn Owl). — Bare, light brown bristles up to 18 mm long behind nostrils, projecting forward nearly to front of beak. Smaller bristles with basal barbs on malar region. Contour feathers on tarsus, or leg, grade into semibristles, which in turn grade into typical bare bristles on the toes (Figure 21); the transition involves a thickening of the rachis from the base upward, and a reduction of vanes from the tip downward.

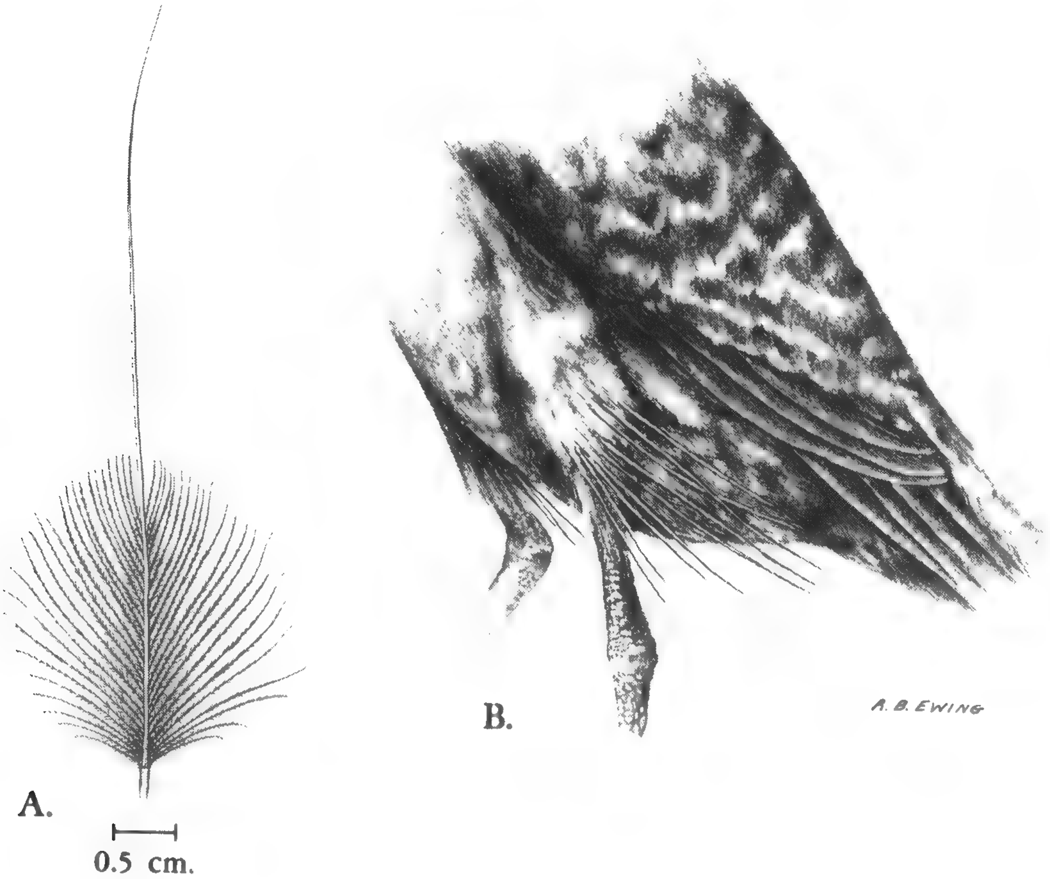

Figure 18. Bristle-thighed Curlew, *Numenius tahitiensis*. A. Bristle-like feather from knee. B. Side view of body showing bristle-like feathers.

Family Strigidae, owls

*Otus asio* (Screech Owl). — Lax contour feathers on the toes grade distally into thin, flexible, unpigmented bristle-like feathers with a few pairs of basal barbs; some of the barbs are nearly as long as the rachis.

*Bubo virginianus* (Great Horned Owl). — Contour feathers grade into a variety of semibristles on the eyelids, facial discs, lores, cere, and gular region (Figure 22). The feathers radiate from the eyes, those in front projecting forward and outward, as is easily seen when the head is viewed from above (Figure 7). The semibristles vary in size from 12 to 27 mm in prominence and stiffness of the rachis, length and spacing of barbs, barbules, and pigmentation. Semibristles on the lores (Figure 6) are typical; those on the cere are more bristle-like. Lax contour feathers on the toes.

*Nyctea scandiaca* (Snowy Owl). — White semibristles up to at least 32 mm long arranged much as in the preceding species.

*Athene noctua* (Little Owl). — Coarse contour feathers of facial discs grade anteriorly into semibristles that project forward beside the beak. "Toes thinly covered with bristle-like feathers" (Witherby *et al.*, 1943).

*Strix varia* (Barred Owl). — Similar to preceding species, semibristles having a dark rachis and pale barbs. Lax contour feathers on toes.

Order Caprimulgiformes

Family Steatornithidae, Oilbird

*Steatornis caripensis* (Oilbird). — Rictal bristles up to 50 mm long (Jany, 1955).

Family Podargidae, frogmouths

*Podargus strigoides* (Tawny Frogmouth). — Coarse contour feathers and semibristles around eyes, on lores, forehead, above rictus, and apex of chin. Semibristles have barbs closely spaced at base, but farther apart and without barbules distally; rachis and apical barbs are black.

Family Aegothelidae, owlet-frogmouths

*Aegotheles insignis* (Rufous Owlet-frogmouth). — A remarkable array of large dark bristles and semibristles on the front of the head (Figure 23). Bristles, with widely spaced bare rami, project ventrolaterally from above the rictus. Several semibristles and two pairs of bristles, up to 35 mm long, curve forward, upward, and outward from the lores. Smaller semibristles are present on the upper eyelids, and below and behind the eyes, forming the facial discs, and on the edge of the gular region.

Family Nyctibiidae, potoos — "No rictal bristles, but loral feathers have bristlelike tips, much elongated and decurved" (Van Tyne and Berger, 1959).

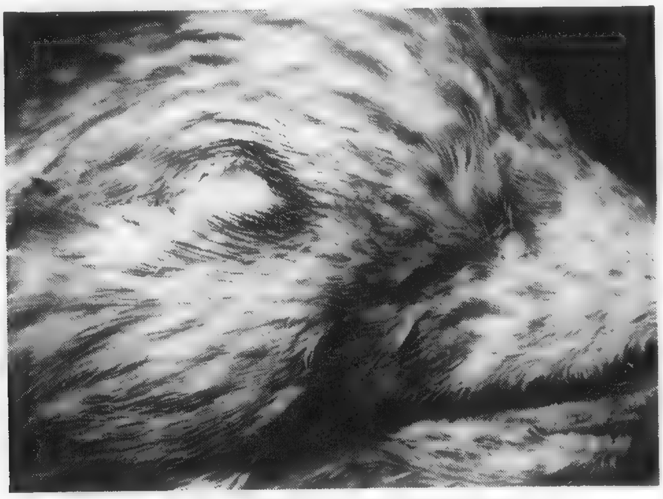

Figure 19. Immature Great Black-backed Gull, *Larus marinus*. Bristles and semibristles in front of eye.

Family Caprimulgidae, nightjars

*Chordeiles minor* (Common Nighthawk). — Semibristles around eyes, on lores, above rictus, and on malar and gular regions; those above the rictus are very short and slender. Semibristles are black distally, with widely spaced barbs along their full length.

*Caprimulgus vociferus* (Whip-poor-will). — Bare black bristles up to at least 41 mm long project forward and outward from above rictus, extending well in front of the tip of the beak. Small semibristles on lores and forehead.

*Caprimulgus longirostris* (Band-winged Nightjar). — Similar to preceding species, but bristles are only up to 32 mm long (Figure 1 E).

Order Apodiformes

Family Apodidae, swifts. — No rictal bristles (Witherby *et al.*, 1943).

*Collocalia esculenta* (Glossy Swiftlet), *Streptoprocne zonaris* (White-collared Swift), *Chaetura chapmani* (Dark-breasted Swift), *C. pelagica* (Chimney Swift), *Cypseloides senex* (Great Dusky Swift), *Apus apus* (Swift). — None.

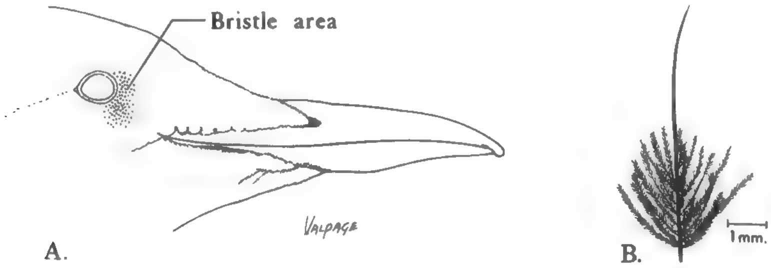

Figure 20. Thick-billed Murre, *Uria lomvia*. A. Side view of head; bristles are located in the stippled area in front of the eye. B. Bristle.

Family Trochilidae, hummingbirds

*Eutoxeres condamini* (Buff-tailed Sicklebill), *Anthracothorax prevostii* (Green-breasted Mango), *Trochilus polytmus* (Streamer-tail). — None.

Order Coliiformes

Family Coliidae, colies, mousebirds
*Colius striatus* (Speckled Mousebird). — None.

Order Trogoniformes

Family Trogonidae, trogons

*Pharomachrus antisianus* (Crested Quetzal. — Stout, black barbed bristles around eyes and projecting forward over nostrils, and from anterior portion of malar and gular regions.

*Trogon mexicanus* (Mountain Trogon), *T. elegans* (Elegant Trogon). — Black bristles, semibristles, and coarse contour feathers around eyes. Upper eyelashes are stout black bristles, some bare and others with a few basal barbs. The orientation of these lashes is reversed, as shown by the fact that the umbilical barbs and the median groove on the rachis, features which are intrinsically on the ventral side of feathers, face uppermost. Also present are a few short, black rictal semibristles, stout narial bristles with long basal barbs, and many black bristles which curve upward from the apex of the chin, on the sides of the lower bill.

Order Coraciiformes

Family Alcedinidae, kingfishers

*Ceryle torquata* (Ringed Kingfisher), *Chloroceryle amazona* (Amazon Kingfisher), *Dacelo gaudichaud* (Rufous-bellied Giant Kingfisher), *Clytoceyx rex* (Shovel-billed Kingfisher).— None.

Family Todidae, todies

*Todus multicolor* (Cuban Tody). — Bristles up to 8 mm long project anterolaterally above rictus and nostrils; bristles are mostly black, but are white at the base, including short barbs. Bristles with unpigmented shaft and red and white barbs, at apex of chin.

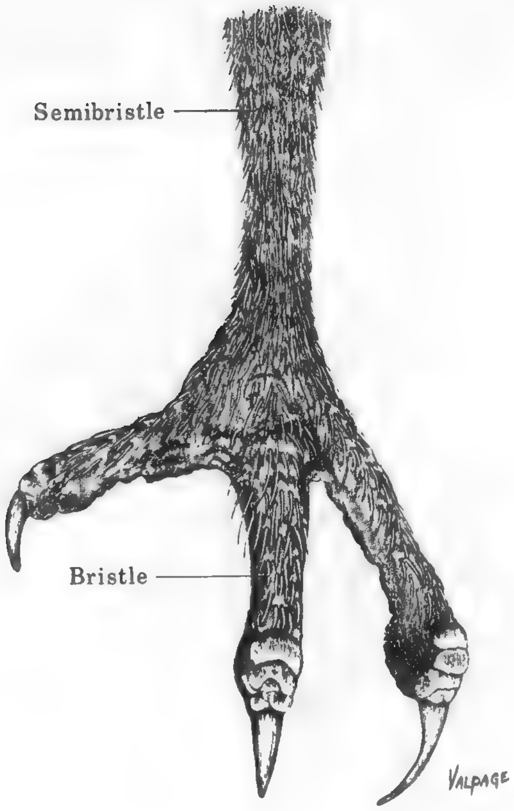

Figure 21. Barn Owl, *Tyto alba.* Toes of right foot.

*Todus subulatus* (Broad-billed Tody). — Similar to preceding species, but bristles are shorter and those on the chin have dark tips.

Family Momotidae, motmots

*Eumomota superciliosa* (Turquoise-browed Motmot). — Black bristles and semibristles on lores and malar region. Semibristles with blue-tipped barbs on chin.

*Momotus momota* (Blue-crowned Motmot). — Similar to preceding species, but also with rictal bristles.

Family Meropidae, bee-eaters. — "Very short, hardly perceptible rictal bristles" (Witherby *et al.,* 1943).

*Merops apiaster* (European Bee-eater). — A few bristles up to 5 mm long above and below rictus, along rear margin of upper bill to nostrils, and on malar region; those below the commissural point have blue-green barbs. Black semibristles below eyes.

Family Coraciidae, rollers

*Coracias garrulus* (European Roller). — Stout, bare bristles up to 7 mm long decurved above rictus. Smaller barbed bristles, some with a tinge of blue, on lores, around eyes, on malar region, and apex of chin.

Family Upupidae, Hoopoe

*Upupa epops* (Hoopoe). — None.

Family Phoeniculidae, wood-hoopoes

*Phoeniculus purpureus* (Green Wood-hoopoe). — None.

Family Bucerotidae, hornbills. — "The margins of the eyelids, especially the upper ones, are furnished with very strong lashes, and . . . these are larger in proportion as the naked space surrounding the eye is extended" (Nitzsch and Burmeister, 1867).

*Tockus nasutus* (Grey Hornbill), *Aceros plicatus* (Papuan Hornbill), *Bucorvus abyssinicus* (Abyssinian Ground Hornbill). — Stout, tapered, bare, black eyelash bristles set close together on rim of upper eyelid (Figure 24). There are about nine eyelashes in *A. plicatus* and at least 18 in *B. abyssinicus.* The median groove on the shaft is uppermost, indicating reversed orientation of the bristles. *A. plicatus* also has black semibristles around the eye.

Order Piciformes

Family Galbulidae, jacamars

*Galbula ruficauda* (Rufous-tailed Jacamar). — Small, bare bristles around eyes. Barbed bristles up to 18 mm long over nostrils and rictus, and on malar region. Semibristles on chin.

Family Bucconidae, puffbirds

*Bucco capensis* (Collared Puffbird). — Small, bare eyelash bristles. A row of dark-tipped decurved barbed bristles along rear edge of upper bill from rictus to nostrils. Semibristles on lores.

*Malacoptila fusca* (White-chested Puffbird), *M. semicincta* (Semicollared Puffbird). — Barbed bristles around eyes. Large black semibristles over nostrils and on lores. Large bristles above rictus and on chin (Figure 25).

Family Capitonidae, barbets. — "Most species have tufts of feathers over the nostrils and/or well-developed rictal and chin bristles" (Van Tyne and Berger, 1959).

*Capito maculicoronatus* (Spot-crowned Barbet). — Bristles along rear edge of upper bill from rictus to nostrils.

*Tricholaema hirsutum* (Hairy-breasted Toothbill), *Lybius rolleti* (Black-breasted Barbet). — Large bristles above the rictus, on the malar region, and on the chin project more or less forward beside the bill (Chapin, 1939).

*Trachyphonus purpuratus* (Yellow-billed Barbet). — Stout semibristles and bristles, some with red rami, in front of lores close to rear edge of upper bill — not truly above rictus. Also present behind nostrils, on malar region, and apex of chin.

Family Ramphastidae, toucans

*Aulacorhynchus haematopygus* (Crimson-rumped Toucanet). — Small black bristles in a row between eyes and base of bill point outward or downward and backward; they grade ventrally into semibristles and contour feathers with blue-green barbs.

*Pteroglossus sanguineus* (Stripe-billed Araçari). — Barbed black bristles up to 6 mm long between eyes and rear edge of bill, grading ventrally into semibristles by addition of barbs and barbules, and thinning of rachis.

*Pteroglossus aracari* (Black-necked Araçari). — None.

*Andigena hypoglauca* (Gray-breasted Mountain Toucan). — Black bristles and semibristles in a diagonal row across bare skin in front of eyes.

*Ramphastos toco* (Toco Toucan). — None.

Family Picidae, woodpeckers, piculets, wrynecks

*Colaptes auratus auratus* (Yellow-shafted Flicker).—Semibristles project over nostrils. Thin, dark-tipped barbed bristles and semibristles up to 6 mm long along rear edge of upper bill, malar region, and edges of chin.

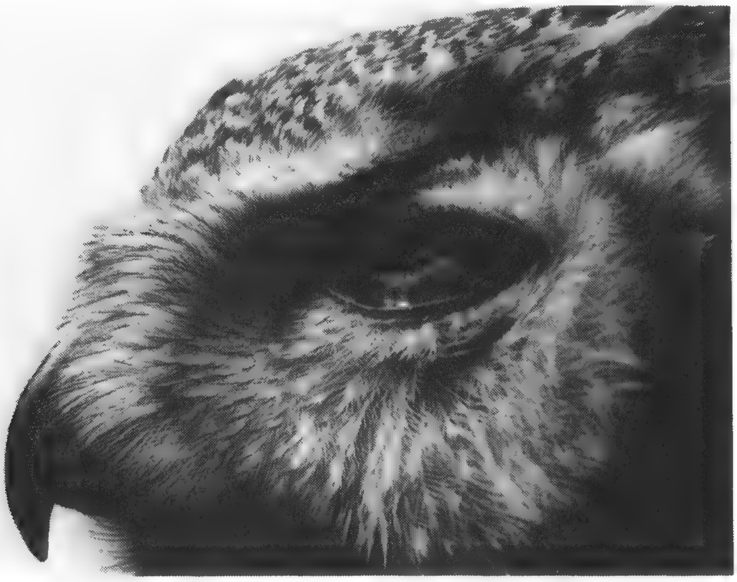

Figure 22. Great Horned Owl, *Bubo virginianus*. Semibristles on eyelids, facial discs, lores, cere, and gular region.

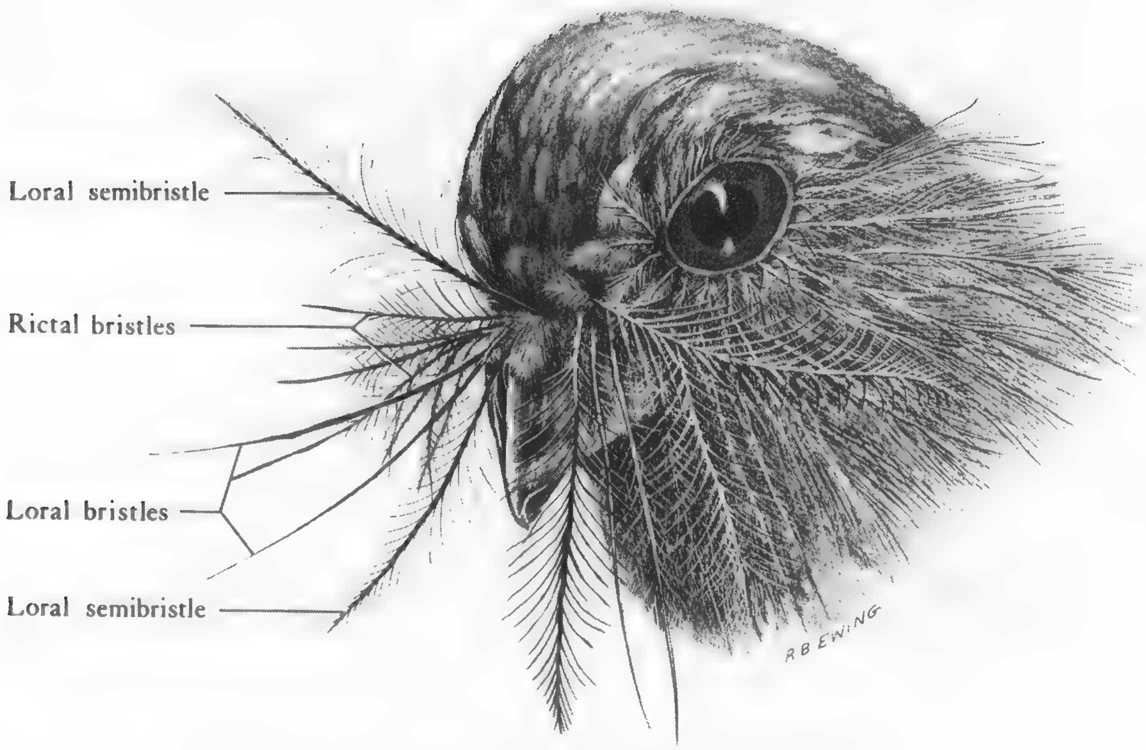

Figure 23. Rufous Owlet-frogmouth, *Aegotheles insignis.*

*Dryocopus pileatus* (Pileated Woodpecker), *D. lineatus* (Lineated Woodpecker). — Dark-tipped bristles with pale barbs project over nostrils and downward from apex of chin (Figure 26).

*Sphyrapicus varius* (Yellow-bellied Sapsucker). — Black-tipped bristles with many barbs — almost semibristles — project over nostrils. Black malar and gular bristles.

Order Passeriformes

Family Eurylaimidae, broadbills

*Cymbirhynchus macrorhynchos* (Black and Red Broadbill). — Stout, barbed, black bristles up to 20 mm long in a row close in front of the eyes, from the commissural point — where the upper and lower mandibles come together — to the rear edge of the upper bill. Black malar and gular bristles.

Family Formicariidae, antbirds

*Taraba major* (Great Antshrike). — Black semibristles below eyes and on lores as far as rear edge of upper bill.

Family Cotingidae, cotingas

*Lipaugus unirufus* (Rufous Piha). — Stout, barbed brown bristles along rear edge of upper bill from above the rictus to behind the nostrils. At first glance, the bristles appear to form a continuous series, but actually they are in two groups, a feature also seen in many of the following passerines. The posterior, or rictal, group, starts with very short bristles just anterior to the commissural point and continues with increasingly longer — up to 9 mm — bristles, about up to the transition from the rictus to the tomium proper; the bristles in this group project ventrolaterally and progressively more forward (Figure 27). The anterior, or narial, group starts with short bristles where the posterior group ends, and continues with longer bristles along the edge of the forehead, and ends near the culmen; these bristles also start projecting laterally and point progressively more forward but they are also decurved over the sides of the bill or the nostrils. Bristles are also present on the lores, lower eyelids, below the infraocular apterium, on the malar region, and on the apex of the chin.

*Querula purpurata* (Purple-throated Fruitcrow). — Stout black bristles below eyes, above rictus, on malar region, and chin.

*Pyroderus scutatus* (Red-ruffed Fruitcrow). — Stout black bristles up to 17 mm long above rictus, on malar region, and chin.

*Rupicola peruviana* (Andean Cock-of-the-Rock). — None.

Family Pipridae, manakins

*Chiroxiphia linearis* (Long-tailed Manakin). — Black barbed bristles up to 5 mm long above rictus and nostrils, on malar region, below infraocular apterium, and on edges of chin.

Family Tyrannidae, tyrant-flycatchers. — "Rictal bristles typically well developed" (Van Tyne and Berger, 1959).

*Tyrannus tyrannus* (Eastern Kingbird). — Stout black rictal and narial bristles with a few widely spaced basal rami. Small bristles on malar region; black-tipped bristles at apex of chin grade posteriorly into semibristles.

*Empidonax virescens* (Acadian Flycatcher). — Black rictal and narial bristles with vestigial barbules on rachis. Bristles on edge of malar region and chin; small loral semibristles with black-tipped barbs.

Family Oxyruncidae, Sharpbill

*Oxyruncus cristatus* (Sharpbill). — "Short, fine bristly feathers at the base [of the bill]" (Van Tyne and Berger, 1959).

Family Menuridae, lyrebirds

*Menura superba* (Superb Lyrebird). — Stout, dark brown, barbed rictal and narial bristles up to 11 mm long grade upward into semibristles and bristles that project outward from the lores and forehead. Bristles all around eyes, varying in size and amount of barbs; skin around eyes is otherwise bare. Malar and gular bristles.

Family Pittidae, pittas

*Pitta reichenowi* (Green-breasted Pitta). — Short rictal bristles (Chapin, 1953).

*Pitta nipalensis* (Blue-naped Pitta). — Pale rictal, malar, and gular bristles.

Family Alaudidae, larks

*Eremophila alpestris* (Horned Lark). — Short, black barbed bristles close together above rictus and behind nostrils.

Family Hirundinidae, swallows, martins

*Tachycineta bicolor* (Tree Swallow), *Progne chalybea* (Gray-breasted Martin), *Hirundo rustica* (Barn Swallow). — Black barbed rictal and malar bristles up to 2 mm long.

Family Campephagidae, cuckoo-shrikes

*Coracina robusta* (Little Cuckoo-shrike). — Black bristles above rictus, below eyes, on malar region, and chin.

Family Pycnonotidae, bulbuls. — "Rictal bristles usually well developed" (Van Tyne and Berger, 1959).

*Hypsipetes amaurotis* (Chestnut-eared Bulbul). — Stout, bare, black rictal and narial bristles up to 10 mm long. Barbed malar and gular bristles grade into semibristles.

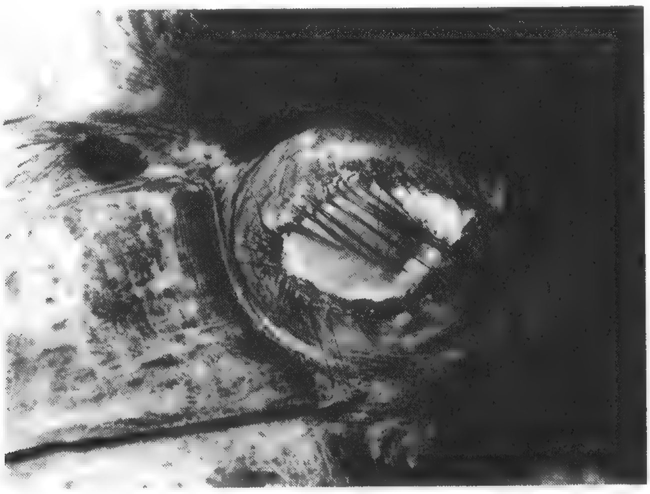

Figure 24. Papuan Hornbill, *Aceros plicatus*. Eyelash bristles.

Family Irenidae, fairy-bluebirds, leafbirds

*Irena puella* (Blue-mantled Fairy-bluebird). — Stout, black rictal and narial bristles up to 6 mm long. Smaller malar and gular bristles.

Family Laniidae, shrikes, helmet-shrikes

*Lanius schach* (Rufous-backed Shrike), *L. excubitor* (Grey Shrike). — Black barbed rictal bristles, up to 11 mm long in *schach,* seven mm in *excubitor*. Numerous shorter barbed, black narial bristles, decurved over sides of bill and nostrils; these grade into loral semibristles.

Family Bombycillidae, waxwings, silky-flycatchers

*Bombycilla cedrorum* (Cedar Waxwing). — Black rictal and narial bristles up to 3.5 mm long, each with a dense cluster of umbilical barbs.

Family Motacillidae, wagtails, pipits

*Macronyx croceus* (Yellow-throated Longclaw). — Bare, black bristles up to 10 mm long project forward and outward above the rictus. Black-tipped bristles and semibristles on lores and below infraocular apterium. Tiny barbed bristles on lower rim of eyes.

*Anthus spinoletta* (American Pipit). — Small barbed bristles and semibristles on lores, malar region, and below eyes.

Family Cinclidae, dippers

*Cinclus mexicanus* (Mexican Dipper). — None.

Family Troglodytidae, wrens — "Rictal bristles wanting or weak and few" (Witherby, *et al.,* 1943).

*Thryomanes bewickii* (Bewick's Wren), *Troglodytes troglodytes* (Winter Wren). — Semibristles with dark, bare-tipped barbs on lores and chin.

Family Mimidae, thrashers. — "Rictal bristles reduced but always present" (Van Tyne and Berger, 1959).

*Dumetella carolinensis* (Gray Catbird). — Several bare, black rictal bristles up to 8 mm long. Smaller barbed bristles on lores, malar region, and chin.

Family Prunellidae, accentors

*Prunella modularis* (Dunnock). — Black rictal bristles grade into brown semibristles with black tips at commissural point and in front of eyes; semibristles have widely spaced barbs, and project outward. Barbed bristles on chin and edge of nostrils.

Family Muscicapidae

Subfamily Turdinae, thrushes. — "Rictal and nasal bristles often distinct but not as strongly developed as in Muscicapidae [= Muscicapinae]" (Witherby *et al.,* 1943).

*Catharus mustelina* (Wood Thrush). — Barbed black bristles in two distinct series, rictal bristles up to 6 mm long projecting laterally to anterolaterally, and narial bristles, which are shorter, thinner, and more laterally directed. White semibristles with bare black tips to barbs on lores, malar region, and chin.

*Turdus migratorius* (American Robin). — Similar to preceding species, the rictal bristles up to 7 mm long and with four or five pairs of short basal barbs (Figure 1 A). Barbed black bristles about 4 mm long on anterior part of malar region. Stiff, black barbed bristles up to 2.5 mm long on lower eyelids.

Subfamily Timaliinae, babblers

*Chamaea fasciata* (Wrentit). — Long, slender rictal and narial bristles.

Subfamily Muscicapinae, Old World flycatchers. — "Strongly developed rictal bristles and bristles more or less covering nostrils" (Witherby *et al.,* 1943).

*Muscicapa hypoleuca* (Pied Flycatcher). — Rictal and narial bristles; smaller bristles and semibristles on malar region and edge of chin.

Subfamily Sylviinae, Old World warblers. — "Rictal bristles variable, obsolete to fairly strong" (Witherby, *et al.,* 1943).

Subfamily Malurinae, Australian warblers

*Dasyornis* spp. (bristle-birds). — The generic name as well as the vernacular name refers to the "two or three strong bristles which curve up and out from the base of the bill" (Hill, 1967).

Family Climacteridae, Australian tree-creepers

*Climacteris leucophaea* (White-throated Tree-creeper). — Semibristles up to 3 mm long project anterolaterally above rictus and anteriorly, as far as the rear end of the nostrils; apical barbs have bare black tips and are about as long as the rachis. Semibristles at apex of chin.

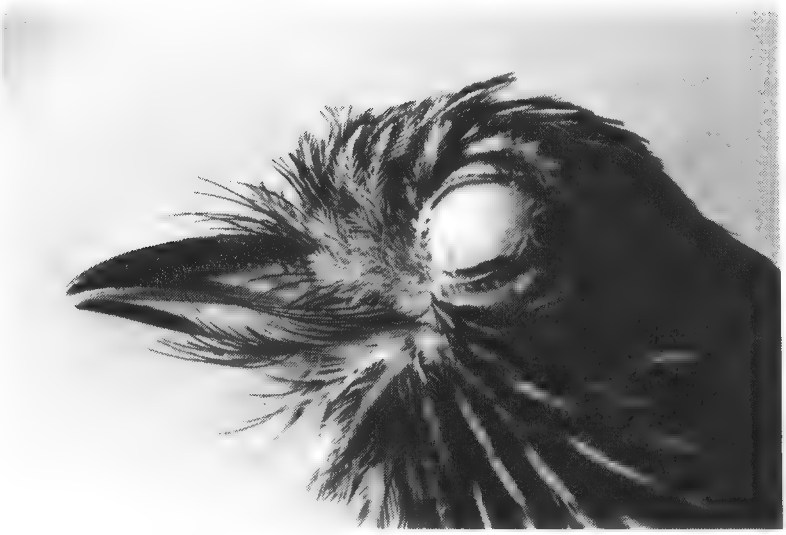

Figure 25. Semicollared Puffbird, *Malacoptila semicincta.* Rictal and gular bristles, narial and loral semibristles.

Family Certhiidae, creepers

*Certhia familiaris* (Brown Creeper). — None.

Family Sittidae, nuthatches

Sitta carolinensis (White-breasted Nuthatch). — Bristles along rictus, and densely present over nostrils and edges of chin; bristles are black distally, white on proximal portions of rachis and barbs. White semibristles with bare black tips on lores and in front of eyes.

Family Paridae, titmice. — "Rictal bristles not very conspicuous, but generally present, though sometimes obsolete" (Witherby *et al.*, 1943).

*Parus atricapillus* (Black-capped Chickadee). — Black rictal and narial bristles and semibristles.

Family Dicaeidae, flowerpeckers

*Dicaeum trigonostigma* (Orange-breasted Flowerpecker). — Black barbed bristles along rear edge of upper bill from commissural point to nostrils. Malar and gular bristles with pale barbs. Black semibristles project outward on lores.

Family Nectariniidae, sunbirds

*Anthreptes malacensis* (Plain-throated Sunbird). — Small black-tipped white semibristles on lores. Larger, up to 3 mm, semibristles project outward on malar region and chin.

*Anthreptes collaris* (Collared Sunbird). — Slender black bristles with reduced basal barbs above rictus, on malar region, and apex of chin.

*Nectarinia cyanolaema* (Blue-throated Brown Sunbird), *N. jugularis* (Olive-backed Sunbird). — None.

Family Meliphagidae, honey-eaters

*Meliphaga melanops* (Yellow-tufted Honey-eater). — Black semibristles with bare tips densely set on lores, up to nostrils. Yellow semibristles with bare black tips on malar region and chin.

*Anthochaera paradoxa* (Yellow Wattle-bird). — A few bristles with short basal barbs just posterior to nostrils. Many dark-tipped semibristles projecting outward on sides and underside of head.

Family Oriolidae, Old World orioles

*Oriolus oriolus* (Golden Oriole). — Slender black bristles up to 5 mm long along rear edge of upper bill from nostrils to end of tomium proper. Malar and gular bristles. Black-tipped pale semibristles project outward on lores.

Family Dicruridae, drongos. — "Generally speaking, the rictal bristles in drongos are well developed and are about from one-half to two-thirds of the length of the bill" (Vaurie, 1949).

*Dicrurus paradiseus* (Large Racket-tailed Drongo). — Stout, bare, black rictal bristles up to 20 mm long. Shorter narial bristles with stiff barbs. Black semibristles on lores and forehead. Malar and gular bristles and semibristles up to 9 mm long.

Family Grallinidae, Australian mud-nest-builders

*Grallina cyanoleuca* (Mudlark). — Four stout bristles up to 9 mm long, with minute barbs, at transition from rictus to tomium proper. Black-tipped white semibristles on lores, in front of and below eyes, on malar region, and chin.

*Corcorax melanorhamphos* (White-winged Chough). — Black semibristles and coarse contour feathers on lores, above rictus, below eyes, on malar region, and chin.

Family Artamidae, woodswallows

*Artamus leucorhynchus* (White-breasted Woodswallow). — Barbed black bristles along rear edge of upper bill from commissural point to nostrils. Semibristles at apex of chin.

Family Cracticidae, bellmagpies, piping-crows

*Strepera graculina* (Pied Currawong). — Black rictal bristles up to 21 mm long. Narial and gular bristles. Loral semibristles.

*Pityriasis gymnocephala* (Bornean Bristlehead). — This curious bird is treated here in the Family Cracticidae, following Thompson (1966), instead of in the Laniidae (Rand *in* Mayr and Greenway, 1960). The English name of the species may refer either to the so-called bristles on the top of the head or to the feathers below the ear region and on the jugulum. In fact, however, there are no bristles. The top of the head is covered with a thatch of filamentous warts 3 to 4 mm long in a museum skin of an adult. "In life these wart-like structures are fleshy and are of a golden orange coloration" (M. C. Thompson, pers. commun.). Some specimens show a few tiny red contour feathers amidst the warts.

Below each ear is a conspicuous patch of closely packed stiff narrow feathers, each about 7 to 9 mm long. These are contour feathers because they have barbs all along the rachis, but the barbs are very short and are curled underneath lengthwise. Each barb consists of a wide ramus and vestigial barbules. The exposed portion of most of these feathers is dark brown whereas the concealed basal portion is red, matching the ordinary contour feathers around the neck. The brown color is not inherent, however, but is due to dirt or some other material that adheres to the underside of the barbs. When this material is scraped off with the tip of a fine scalpel, the barbs are colorless. Those few feathers with pale exposed portions are apparently fresh and have not yet acquired their brown coating.

The "bristly" feathers on the jugulum are also contour feathers, similar to those just described but larger — about 17 mm long — and less highly modified. When the adherent brown material is scraped from the barbs at the tip of a feather, the rami are red. The tips of fresh feathers are reddish brown, not dark brown as are the older feathers.

Family Ptilonorhynchidae, bowerbirds

*Sericulus chrysocephalus* (Regent Bowerbird). — Small rictal, loral, malar, and gular bristles and semibristles.

Family Paradisaeidae, birds of Paradise

*Cicinnurus regius* (King Bird of Paradise), *Paradisaea minor* (Lesser Bird of Paradise). — None.

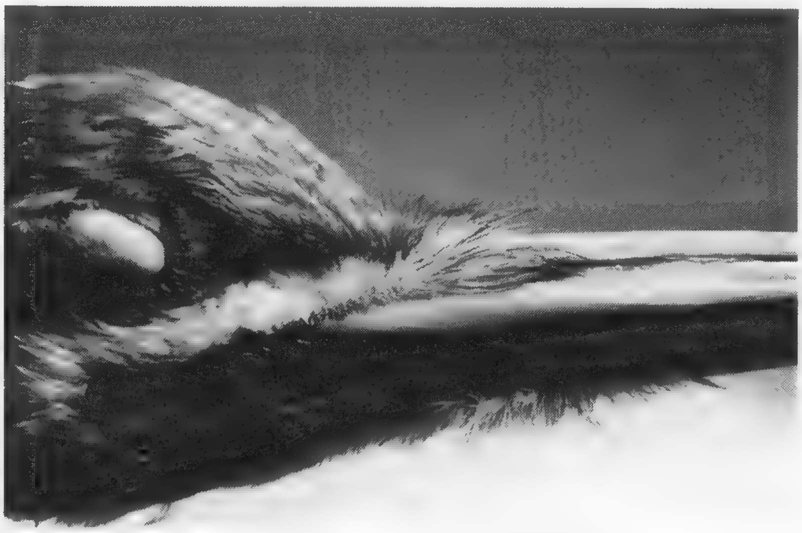

Figure 26. Pileated Woodpecker, *Dryocopus pileatus*. Narial and gular bristles.

Family Corvidae, crows, jays, magpies

*Gymnorhinus cyanocephala* (Piñon Jay). — Slender black rictal bristles up to 7 mm long. Smaller narial bristles. Black semibristles project outward on lores. Malar and gular bristles and semibristles, some with structurally blue barbs.

*Cyanocitta cristata* (Blue Jay). — Black rictal bristles up to 11 mm long (Figure 4). Semibristles with a black rachis and widely spaced blue and white barbs project over the nostrils. Bristles and semibristles with a black rachis and white barbs curve outward from the lores, malar region, and chin.

*Garrulus glandarius* (Jay). — Black rictal bristles up to 12 mm long. Narial semibristles. Eyelash bristles all around eyes. Semibristles on lores, below eyes, on black malar stripe, and on chin. Bristles on anterior malar region.

*Nucifraga columbiana* (Clark's Nutcracker). — Black-tipped pale semibristles above rictus, below eyes, on malar region, and chin. Coarse contour feathers without barbules project over nostrils.

*Corvus brachyrhynchos* (Common Crow), *C. ossifragus* (Fish Crow). — Black rictal bristles with a few small barbs. Slender, stiff, black narial semibristles about 20 mm long with barbs widely spaced along entire rachis; barbules on proximal portions of barbs. Barbed black bristles project outward on lores, around eyes, on malar region, and chin. Contour feathers on upper eyelids show tendency toward bristle structure in elongate rachis, long bare tips of barbs, and clustering of barbs at base.

Family Sturnidae, starlings, mynahs

*Spreo bicolor* (Pied Starling). — Black bristles up to 8 mm long along rear edge of upper bill from behind nostrils to end of tomium proper; these grade into black semibristles on the lores. Black malar and gular semibristles.

*Sturnus vulgaris* (Common Starling). — Black rictal bristles 4 to 5 mm long with umbilical barbs and several pairs of shaft barbs (Figure 1 B). Upper eyelash bristles 2 mm long, with dense cluster of barbs sometimes shielding external feather caps (Figures 1 D, D′).

Family Ploceidae, weavers

*Passer domesticus* (House Sparrow). — Bare, black rictal and narial bristles up to 6 mm long, the longest at the transition from the rictus to the tomium proper. Short, black semibristles on lores, malar region, and chin. Semibristles with gray barbs below infraocular apterium.

Family Estrildidae, waxbills, mannikins, grassfinches

*Chloebia gouldiae* (Gouldian Finch). — None.

Family Fringillidae, cardueline finches

*Carduelis pinus* (Pine Siskin). — Several black-tipped rictal semibristles up to 4 mm long, with about three pairs of widely spaced bare rami. Dark brown-tipped narial bristles up to 2.5 mm long with widely spaced basal barbs and vestigial barbules. Loral semibristles up to 2.5 mm long, with black bare tips. Malar and gular semibristles up to 5.5 mm long.

*Carduelis carduelis* (European Goldfinch). — Similar to preceding species except for semibristles instead of bristles over nostrils.

*Carpodacus purpureus* (Purple Finch). — Black-tipped rictal and narial bristles up to 4 mm long. Loral, malar, and gular semibristles.

*Loxia curvirostra* (Red Crossbill). — Pale semibristles along rear edge of upper bill, on lores, malar region, and edge of chin.

Family Vireonidae, vireos, peppershrikes, shrike-vireos

*Vireo olivaceus* (Red-eyed Vireo). — Black, bare rictal bristles up to 5.5 mm long project forward and slightly upward. Black narial bristles with pale basal barbs, up to 4.2 mm long, curl forward and downward. A gap about 2.5 mm separates the two series. Black-tipped bristles and white semibristles on the malar region and chin.

Family Parulidae, New World warblers.—"A few species have . . . pronounced rictal bristles" (Van Tyne and Berger, 1959).

*Mniotilta varia* (Black-and-white Warbler). — Black-barbed rictal bristles up to 4 mm long. Narial bristles similar but smaller. White semibristles with bare black tips project outward on lores, malar region, and chin.

*Dendroica coronata* (Myrtle Warbler). — Similar to preceding species, with rictal bristles up to 6 mm long. Coarse black contour feathers on the lores, and bristles with white bases on the malar region.

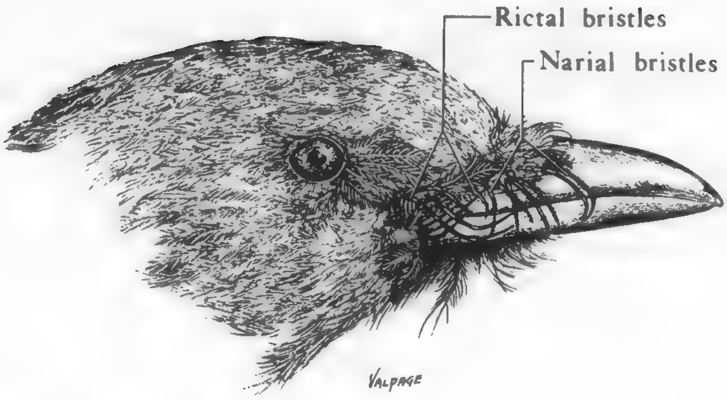

Figure 27. Rufous Piha, *Lipaugus unirufus.*

Family Emberizidae, tanagers, buntings, New World sparrows, cardinal-grosbeaks, plush-capped finch

*Zonotrichia melodia* (Song Sparrow). — Barbed black-tipped rictal bristles up to 5.5 mm long; miniature contour feathers grade into these bristles by reduction in numbers of barbs and in size of barbules, thickening of rachis, greater spacing between barbules, and darkening. Pale semibristles with black tips on chin and edge of malar region; black-tipped brown semibristles project outward on lores and below eyes.

*Pipilo erythrophthalmus* (Rufous-sided Towhee). — Barbed, black rictal and narial bristles up to 6 mm long. Black semibristles below eyes and on malar region. Gular bristles and semibristles.

*Pheucticus ludovicianus* (Rose-breasted Grosbeak). — Bare black bristles up to 5 mm long along rear edge of upper bill from above rictus to nostrils. Barbed bristles at anterior end of malar region and on edge of chin.

*Piranga olivacea* (Scarlet Tanager). — A few small black rictal and narial bristles. Black-tipped red semibristles project outward in front of the eyes and on the lores. Malar bristles with black tips and red basal barbs.

*Anisognathus flavinuchus* (Blue-winged Mountain-Tanager). — Black rictal bristles up to 5 mm long. Shorter narial, malar, and gular bristles.

Family Icteridae, troupials, New World blackbirds

*Icterus galbula* (Baltimore Oriole). — Small rictal, narial, malar, and gular bristles. Loral semibristles and tiny semibristles on rim of upper eyelids.

*Sturnella neglecta* (Western Meadowlark). — No rictal or narial bristles or semibristles. Stout, black eyelash bristles up to 5 mm long, with very short yellow basal barbs, close together above and in front of the eyes; these grade into smaller bristles with white barbs below the eyes, and into semibristles on the lores. Many black-tipped bristles with yellow and/or white barbs on the malar region and the edge of the chin.

*Quiscalus quiscula* (Common Grackle). — Black rictal bristles up to 4 mm long. No eyelashes. Iridescent black semibristles project outward, forming a plush on the lores and in front of the eyes. These grade into bristles with basal barbs, below the infraocular apterium.

## *Functions*

The functions of bristles and semibristles, which have received little study, must still be regarded as largely conjectural, based mostly on morphological evidence. Such evidence includes not only the structure and location of these feathers but also their stiffness and wear-resistance, their trait of projecting outward from the surface, and their innervation.

One common thought is that rictal bristles enlarge the gape of the mouth, thereby making the capture of flying insects easier (Mayaud, 1950; Van Tyne and Berger, 1959). I do not know, however, of any published report to substantiate this theory. The fact that rictal bristles are very small or absent in the

Common Nighthawk (*Chordeiles minor*), swifts, and swallows, all preeminent aerial feeders, weakens this idea. Lederer (1972) observed that in tyrant flycatchers the rictal bristles play no part in the capture of flying insects. Downward-projecting rictal bristles and upward-projecting malar and gular bristles — as in jacamars, puffbirds, barbets, and some passerines — may, however, help to retain food in the mouth.

Bristles and semibristles in many birds seem to keep insects and foreign particles out of the nostrils, eyes, or external ear openings. These feathers form a dense screen over the nostrils in woodpeckers, nuthatches, and corvids. Large eyelashes and bristles around the eyes are common, being found in such birds as rheas, Ostrich, Osprey, Secretarybird, caracaras, Hoatzin, Vulturine Guineafowl, Black-legged Seriema, cuckoos, trogons, hornbills, and meadowlarks. In several museum skins of hornbills that I examined, the grooves of the eyelashes were packed with dirt and wood particles, evidence that these feathers do indeed protect the eyes. The external ear openings are usually screened by coarse contour feathers, the ear coverts, but in the Ostrich, emus, and Hoatzin, they are covered or surrounded by semibristles. The semibristles on the Pied-billed Grebe and the modified frontal feathers of certain rails may serve a different sort of protective function in preventing abrasion of the feathers when the birds push through marsh vegetation (Brush, 1967). Hill (1967) suggested that the bristles at the base of the bill in a bristle-bird "might give some protection to the bird's eyes as it pushes through the thick grass and undergrowth."

Large rictal and loral bristles and semibristles have long been thought to be tactile, or touch, structures in some birds, analogous to the whiskers of cats and mice. In owls, vibration and pressure receptors, the avian lamellar (Vater-Pacini, Herbst) corpuscles, are more numerous around the follicles of loral bristles than in feathered skin elsewhere (Küster, 1905). A microscopic section of the skin in front of the eye of a young Great Horned Owl shows several sections of corpuscles beside each follicle (Figure 28), whereas in the body skin of domestic chickens and ducks there are only a few. The corpuscles vary morphologically in different parts of the body (Malinovsky, 1967), suggesting that a comparison of those at the bases of the bristles with those in other sites might be revealing. The relative abundance of lamellar corpuscles in owl loral skin supports the idea that large rictal and loral bristles and semibristles of some birds help to detect nearby prey, obstacles, or the sides of the nesting or roosting cavity. This appears to be especially likely in crepuscular or nocturnal birds such as kiwis, owls, and caprimulgiforms. Semibristles, as in owls and owlet-frogmouths, having more expanse would seem to be better detectors than bristles.

Jany (1955) suggested that many bristles along the base of the upper beak do not function as mechanoreceptors but as chemoreceptors. He postulated that chemical stimuli received by the end-bodies were conducted through the hollow shaft of the bristles to a central sensory epithelium, a mechanism analogous to the chemoreceptive hairs of insects. There does not seem to be any structural evidence for this theory. Jany did not show that the end-bodies are porous or that they contain branched endings of chemosensory neurons, as do insect chemoreceptors (Case, 1966; Dethier, 1962). Bristles are not hollow except in the calamus, and in owls, at least, there do not appear to be receptor cells at the base (Figure 28).

Bristles and semibristles covering parts of the head appear in some cases to be less easily ruffled, worn, or soiled than ordinary contour feathers (Chandler, 1914). Falconiform birds show a tendency toward reduced feathering in the area immediately around the bill, and in vultures the head is almost bare (Brown and Amadon, 1968). This is related to the fact that most of these birds eat gory food, some feeding on carrion, and a few on slimy snails. The lack of feathers, or their replacement by bristles, keeps the head from being smeared and matted with blood. The same principle may also apply to the bristles and bristle-like feathers on the toes of owls.

Short bristles on the otherwise bare head and neck of birds which are not carrion-feeders — for example, rheas, Ostriches, emus, cassowaries—may have become reduced as adaptations to expose the skin for radiation of body heat. Alternatively, bristles sometimes expose brightly colored skin which may function as a visual signal, as in turkeys, guineafowl, certain cranes, and Roadrunners.

In a few cases, the bristles themselves appear to be visual signals. Crowned Cranes seem to use their cluster of bristles on the crown in displays for defending territory and maintaining the pair-bond (L. H. Walkinshaw, pers. commun.). The pattern of bristles on the head of the King Vulture and the so-called "bristles" below the ears and on the jugulum of the Bornean Bristlehead are so conspicuous that they, too, seem to contribute to the bird's appearance.

I find it difficult to account for the short bristles and semibristles on the lores and in front of the eyes of many charadriiform and passeriform birds. These feathers are usually inconspicuous, and their shortness renders it unlikely that they have a tactile function. Their location and the fact that they usually project outward suggest that in some way they protect the eyes when the birds are in flight.

## *Conclusions*

Far from being confined to a few groups, bristles occur in many kinds of birds. They are usually stiff, bare, and dark, at least at the tip. At the same time, several structures which are commonly called bristles are not truly such — such as ptarmigan toe feathers, turkey beard fibers, thigh feathers of the Bristle-thighed Curlew, and the warts and special head feathers of the Bornean Bristlehead. Bristles, semibristles, and bristle-like structures undoubtedly have adaptive significance, but in most cases this is hardly known. These feathers often appear to play different roles in different parts of the body. Even those in the same location sometimes play different roles in different birds — for example, the rictal bristles of kiwis and barbets.

The pattern of the occurrence of bristles in orders of birds says little about the evolution of these feathers. The bristles of ratites (rheas, Ostriches, emus, cassowaries, and kiwis) seem to be as highly developed as those of passerines. The virtual absence of bristles in the orders Podicipediformes through Ciconiiformes, and their apparent absence in loons, kingfishers, and dippers suggest that aquatic habits preclude the formation of bristles. The presence of bristles in charadriiforms, and their absence in certain non-aquatic groups such as pigeons weakens this conclusion. Bristles in different groups of birds have probably arisen many times, as indicated by the variation in the occurrence and structure. The transitional feathers between contour feathers and bristles show that bristles have evolved from contour feathers. Hence, bristles attest to the plasticity of contour feather germs.

Bristles do not appear to be useful taxonomic characters at the ordinal or familial level, but they may prove useful in certain groups at lower levels.

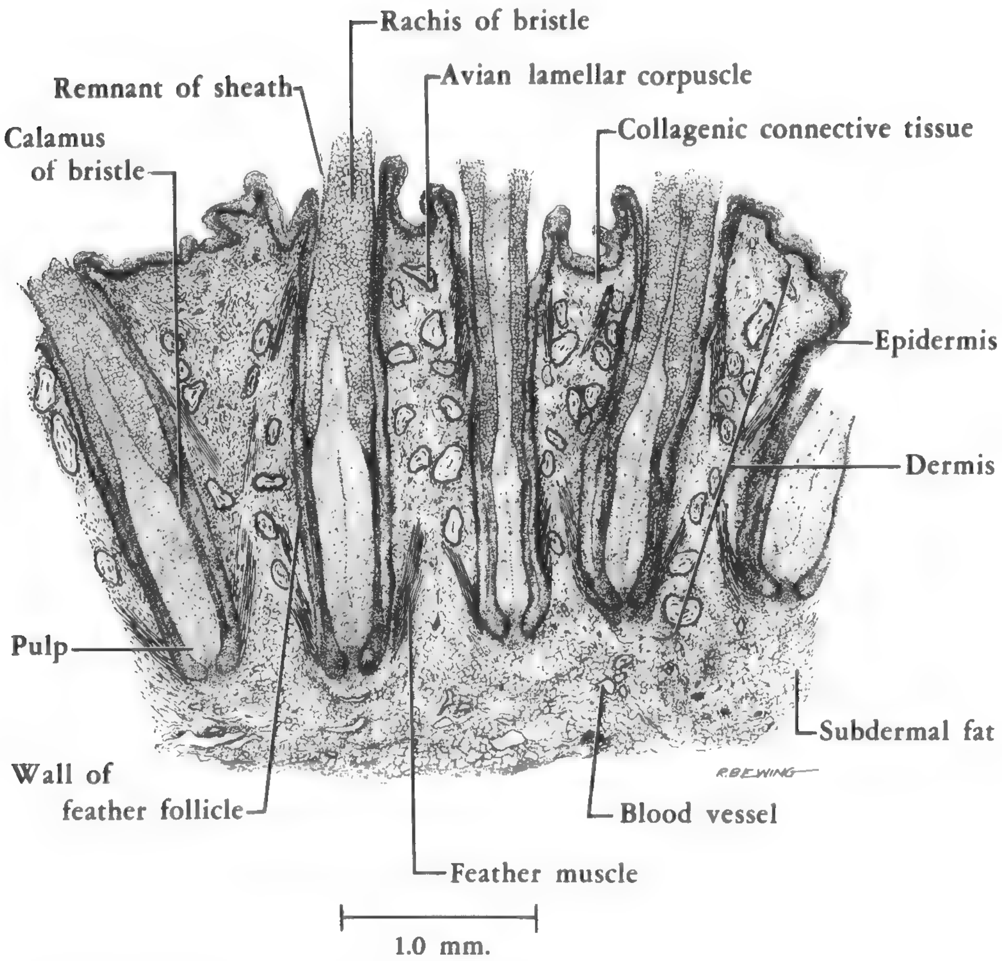
Rachis of bristle
Remnant of sheath
Avian lamellar corpuscle
Calamus of bristle
Collagenic connective tissue
Epidermis
Dermis
Pulp
Subdermal fat
Wall of feather follicle
R.B.EWING
Blood vessel
Feather muscle
1.0 mm.

Figure 28. Cross section of skin in front of the eye of a young Great Horned Owl, *Bubo virginianus*. Bouin's fixative, haematoxylin and eosin staining.

They can vary even at the specific level, as shown by the eyelashes in three species of *Coccyzus* — bristles in one, semibristles in another, and none in a third. We should use bristles cautiously as taxonomic characters, especially until we know more about them.

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## *Glossary*

Analogous — similar in function but of different evolutionary origins.

Apical — at or near the apex.

Barb — a side branch from the shaft of a feather, composed of a main axis and its closely parallel sets of secondary branches, the barbules.

Barbule — a branch of a barb.

Carotenoid — bright red, orange, and yellow fat-soluble pigments; they are synthesized by plants and appear in birds — in a diffused state — after being modified from ingested food.

Caruncle — a fleshy protuberance of the skin, usually on the head or neck. Caruncular — having caruncles.

Cathartid vultures — New World vultures, members of the Family Cathartidae; they differ from Old World vultures in having perforate nostrils and weakly raptorial feet.

Cere — the fleshy covering of the proximal part of the upper mandible in some orders of birds.

Chemoreceptor — sense-organs or sense-cells that are stimulated by the chemical action of definite substances in contact with them.

Commissural point — the angle of the mouth, the point on each side where the mandibles meet posteriorly.

Culmen — the ridge of the upper mandible — the uppermost, central longitudinal line.

Dermal — formed in the dermis, the lower layer of the skin.

Distal — situated away from the base or the point of origin or attachment.

Epidermal — formed in the epidermis, the upper layer of the skin.

Facial discs — roughly circular arrangements of radiating feathers around the eyes of many owls and caprimulgiform birds.

Feather germ — an embryonic structure in the skin that will give rise to a feather.

Follicle — a pit of epidermis, out of which a feather grows.

Gular — pertaining to the throat.

Infraocular apterium — a patch of bare skin below the eye in some birds.

Jugulum — the foreneck, the area between the gular region and the breast.

Loral region, lore — the area between the eyelid and the base of the upper part of the bill, on each side.

Malar — pertaining to the area on the side of the head from the base of the lower part of the bill to the angle of the jaw; the area lies between the throat and the ear coverts.

Mechanoreceptor — sense-organs or sense-cells that are stimulated by sound, pressure, tension, movement, etc.

Melanin — black, brown, red-brown, and yellow relatively insoluble pigments of high molecular weight; they are synthesized by animals in special cells and are present in microscopic granules.

Narial — pertaining to the nostrils and the area immediately around them.

Occiput — the back part of the head, between the crown and the nape.

Operculum — a flap or membrane covering the nostril in some birds.

Pennaceous — describing the firm, closely-knit texture of contour feather vanes.

Proximal — situated near the base or the point of origin or attachment.

Rachis — the portion of a feather shaft bearing vanes.

Ramus (pl. rami) — the main axis of a barb.

Rictal — pertaining to the rictus, the fleshy posterior part of the edges of the mandibles near the commissural point.

Semiplume — a feather with downy texture — no interlocking barbs — in which the rachis is longer than the longest barb.

Snood — a distensible, fleshy protuberance situated on the base of the upper mandible — above the nasal region — in Common Turkeys.

Supraorbital — pertaining to the region above the eyes.

Tomium — the cutting edge of a mandible.

Tyndall scattering — the phenomenon of causing blue color by the scattered reflection of the shorter waves in white light by very small particles, as in the sky.

Umbilical barbs — barbs that attach to the rim of the superior umbilicus, which is a pit on the underside of a feather shaft at the base of the vanes.

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# ECOLOGY OF SOCIAL ORGANIZATION IN THE BLACK-CAPPED CHICKADEE

JON C. GLASE

The concept of a pecking order, or social dominance-hierarchy, was first developed by Schjelderup-Ebbe (1922) while studying the social behavior of the domestic fowl (*Gallus gallus*). The arrangement within the pecking order was linear and unilateral, with each bird being submissive to all individuals above it in dominance rank and dominating all individuals below it in dominance rank.

Etkin (1964) felt that the use of the term "pecking order" instead of "dominance-hierarchy" was inaccurate because it emphasized only the disruptive, aggressive aspects of that kind of social system. Even Schjelderup-Ebbe (1922) admitted that he observed very little active aggression unless birds were forced to compete for limited and concentrated food sources.

Masure and Allee (1934a) reported a study of the social order within flocks of the domestic fowl and the Rock Dove (*Columba livia*). Although their findings for the fowl agreed well with Schjelderup-Ebbe's earlier work (1922), they found a basically different kind of dominance-hierarchy in pigeon flocks. The dominance relationships between individual pigeons were not unilateral as in the chicken. Instead, a relative dominance existed in which individual "A," although statistically dominant over individual "B," would occasionally lose fights to him. Difficulty also existed in ranking birds into a linear hierarchy because of the existence of fairly permanent dominance triangles, where individual "A" was statistically dominant to individual "B," "B" was statistically dominant to "C," and "C" was statistically dominant to "A." Masure and Allee (1934a) called this dominance hierarchy a "peck-dominance" system and characterized it as a dominance that is relative and non-unilateral with permanent dominance-triangles. The type of hierarchy characterized by unilateral, absolute dominance and a linear hierarchial structure Masure and Allee called a "peck-right" system.

Additional laboratory studies have shown that, in some species exhibiting a peck-dominance hierarchy, the outcome of aggressive interactions frequently depends upon the site (Castoro and Guhl, 1958; Masure and Allee, 1934b; Ritchey, 1951), indicating the possibility for interaction between territoriality and social dominance. Brian (1949) studied the Great Tit (*Parus major*) and found that an individual's dominance at a feeder varied inversely with the distance between the feeder and the bird's breeding territory. Brown (1963) found similar results in the social organization of the Steller's Jay (*Cyanocitta stelleri*), but noted that the individual's winter dominance varied inversely with the distance from the site of the encounter to the bird's past nesting area. These and other field studies (Davis, 1942; Greenberg, 1947) seemed to argue for the soundness of Allee's (1938) suggestion that observations at only one location could lead to the misinterpretation of a peck-dominance hierarchial system for one of a peck-right system.

Dixon (1963, 1965) found that the Carolina Chickadee (*Parus carolinensis)* and the Mountain Chickadee (*P. gambeli*) established pack-right hierarchies. Generally, the most dominant individual within the flock, a male, had previously maintained a breeding territory in the winter flock's range. The dominance relationships of the alpha males from three flocks of Mountain Chickadees were of the peck-dominance type, and the outcome of a particular encounter depended upon the location of the encounter relative to the past territorial boundaries during the breeding season. Although he lacked sufficient data to determine if this was also true for the other members of the flock, Dixon felt that the Mountain Chickadee exhibited both types of hierarchies simultaneously, peck-right within flocks and peck-dominance between different flocks. He further suggested that the term "peck-dominance" be dropped, because the concept had developed through laboratory studies of confined vertebrates and had never been demonstrated for a natural, free-roaming group of animals. He agreed with Marler's suggestion (1956) that peck-dominance was a form of territorial behavior, but felt that it was not a basis of organization for natural groups.

## *Objectives of Study*

While my study was in progress, Hartzler (1970) reported that the flock of Black-capped Chickadees he studied for two months displayed a peck-right hierarchy among its members, but he characterized the interactions between flocks as peck-dominance. My study was designed to get at least partial answers to the following questions about the social organization of the Black-capped Chickadee (*Parus atricapillus*):

(1) What is the nature of the dominance hierarchy in winter flocks?

(2) What factors are important in determining the amount of dominance an individual will attain within a flock hierarchy?

(3) How is the dominance hierarchy implemented in a free-roaming flock? Previous field studies relied predominantly on data gathered at artificial feeders. This approach concentrates aggressive behavior, and certainly makes it easier to determine hierarchial systems; but unless naturally foraging flocks also exhibit a similar system, few conclusions can be reached on the ecological significance of social hierarchies. This may be particularly important while studying members of the family Paridae, which are mainly twig and foliage gleaners of insects (Lack, 1971). As such, their natural food is much more dilutely and randomly dispersed throughout the habitat than the concentrated food supply offered by an artificial feeding station. Part of this study was an attempt to understand the structure and implementation of social hierarchies within naturally foraging flocks of birds.

(4) What are the consequences for the individual of participating in this form of social organization? I examined two important phenomena that might possibly be affected by an individual's dominance within a flock:

reproductive success and accessibility to food resources during the flocking period. Although some evidence by Dixon (1963), Odum (1941b, 1942), and Hartzler (1970) indicates that the most dominant males within a flock remain in the area to breed, little quantitative data exist on the possible influence of winter flock dominance on reproductive success. Lack's (1966) view that most bird populations are regulated by food supply in a density-dependent fashion outside of the breeding season and Gibb's (1960; 1962) data on high winter mortality in the Coal Tit (*Parus ater*) suggest that a social hierarchy could be effective in the differential allocation of the food resources available to a flock. Part of this study involved a limited investigation of the foraging niche of chickadees to determine if, and how, the foraging activities of individuals vary with their dominance in the flock.

## *Materials and Methods*

### Study Area

I conducted my study in an area located to the south of Ithaca, New York on the eastern side of a five-mile-long glacial valley. The study area covered an area of 159.7 hectares at an elevation from 280 to 500 meters above sea level. Five general habitat types exist within the study area: woodland, old fields and early successional forests, cultivated fields and pastures, hedgerows, and pond and marsh. Both winter ranges and breeding territories were found predominantly in the first two habitat types. Woodland mostly covers the steeper sides of the valley and comprised about 53.7 percent (99.4 hectares) of the total area. Beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and shagbark hickory (*Carya ovata*) dominate among the tree species, with white oak (*Quercus alba*), basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*) common. The woodland was selectively lumbered in 1951 resulting in a discontinuous canopy in some areas. Old fields and early succession forest represent about 21.3 percent (39.2 hectares) of the study area and contain a wide diversity of both herbaceous and wood plants, including several species of hawthorn (*Crataegus*), pin cherry (*Prunus pennsylvanica*), quaking aspen (*Populus tremuloides*), white pine (*Pinus strobus*) seedlings, numerous old field annuals and perennials, in addition to several old apple orchards. About 18.6 per cent of the study area is currently under cultivation or used for pasture. Flocks and breeding pairs were frequently found in the hedgerows (1.2 percent, 2.2 hectares) surrounding much of this farm land. A large beaver pond and associated marsh, representing 5.1 per cent (9.6 hectares) of the study area, is located in the southern sector.

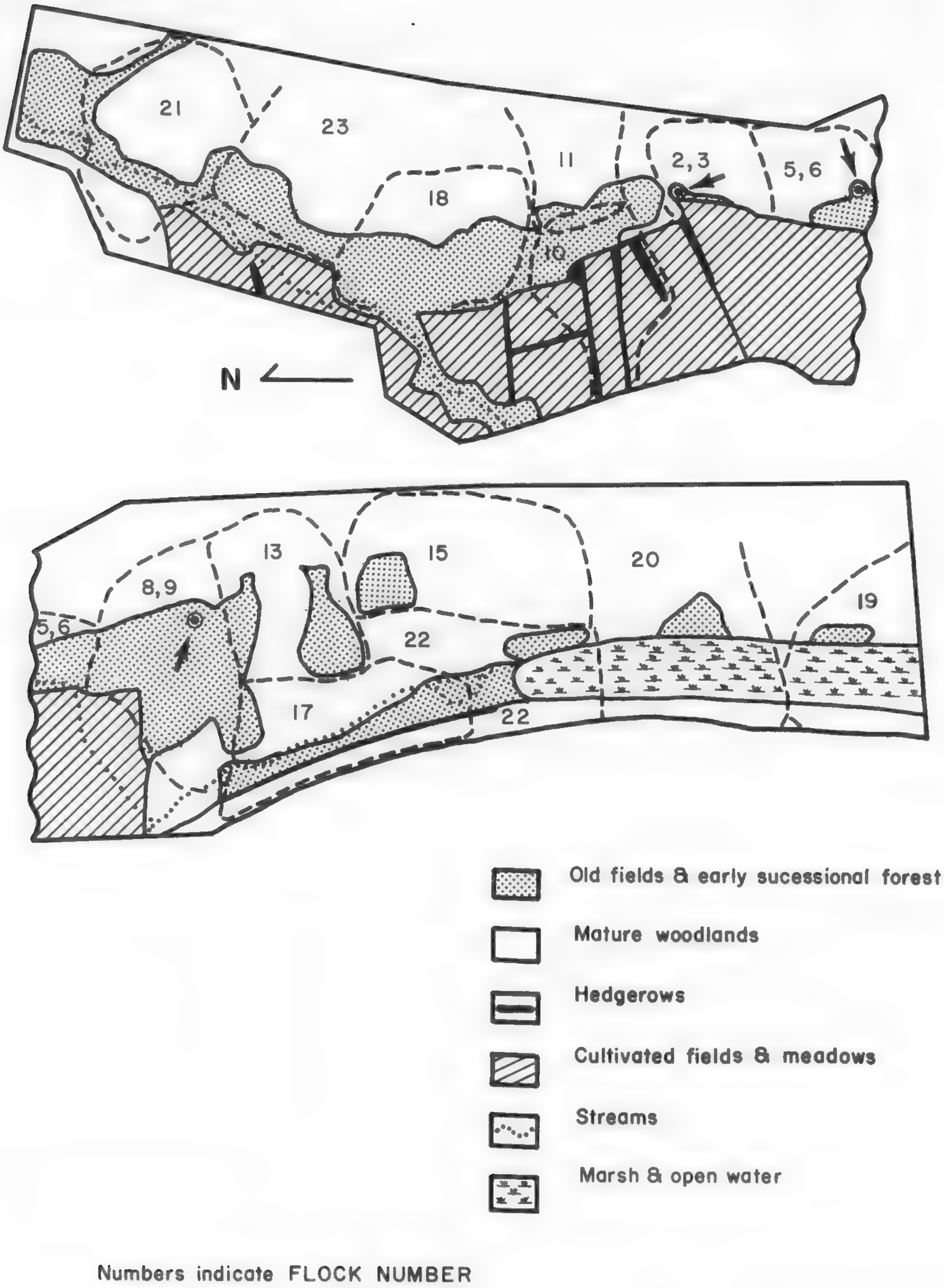
### Capturing and Banding

I captured birds with mist nests placed between feeders and surrounding vegetation. During July and August I set many mist nests elsewhere because chickadees ignored feeders prior to September. Each captured bird received a unique combination of from one to three color bands (celluloid split-ring) in addition to a Fish and Wildlife Service aluminum band. I weighed each bird on a triple beam balance, measured the wing cord with the wing flattened, and determined the degree of pneumatization of the cranium, all of which are important in determining the age and sex. Appendix I presents a more detailed explanation of the methods used to age and sex Black-capped Chickadees.

### Monitoring Flock Activities

During the first two winters I operated three large hopper-type feeders about one-half the time (see Figure 1 for locations). During the third winter I placed a simple platform feeder in the ranges of each of the ten flocks studied that year. In order to minimize the disruptive effects that feeders have on the natural distribution of flocks, I replenished each of these feeders only prior to studying that particular flock.

When feeders were not baited, I studied the distribution and activities of free-roaming flocks. I identified individual members of these flocks by their color bands and plotted the flock's movements on several large scale aerophotos of the study area. I made an estimate of the amount of natural aggression occurring within free-roaming flocks by


21
23
11
2,3
5,6
18
10
N
13
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20
8,9
5,6
19
22
17
22
Old fields & early sucessional forest
Mature woodlands
Hedgerows
Cultivated fields & meadows
Streams
Marsh & open water
Numbers indicate FLOCK NUMBER

Figure 1. Map showing the habitat of the study area near Ithaca, New York and the flock ranges of Black-capped Chickadees (dotted lines).

noting the number of agonistic interactions seen in a given period of time. Because the "dominance call" described by Odum (1941b) was known to be involved in agonistic encounters, I also monitored its occurrence, even if I could not see the actual interaction. I attempted to observe the participants in, and the outcome of, all interactions. I later compared these data with the dominance of individuals based on observation made at feeders.

## Determination of Dominance Hierarchies

I collected most of the data used to ascertain the dominance of individuals in natural flocks and the feeding aggregations of several flocks while watching birds compete at feeders. I considered "A" the dominant bird in a given interaction if:

(1) bird "A" actively displaced bird "B" from the feeder;

(2) the presence of "A" at the feeder caused "B" to wait (measured in seconds) until "A" left before coming to the feeder;

(3) bird "A" directed at "B" what I defined as a "threat" display (Figure 2), usually causing the threatened bird to leave or to respond with an "appeasement" display;

(4) bird "B" directed an "appeasement" display (Figure 2) at "A." These criteria are similar to those used by other workers (Brown, 1963; Dixon, 1965; Hartzler, 1970).

I recorded verbal descriptions of the interactions occurring at a feeder on magnetic tape and later transcribed them onto coding sheets. I combined the data from several consecutive days of observation and analyzed them by computer in batches of at least 300 interactions. Based on these interactions, the computer program decided to which individuals each of the birds was dominant and to which it was subordinate. Frequently, no, or too few, interactions had occurred between two birds, so that it was impossible to determine their dominance relationship. In some cases, the dominance relationship was ambiguous, as each bird dominated the other equal numbers of times.

Using the data on all individuals of each flock, I estimated the linearity of each hierarchy. A completely linear hierarchy is one in which individual "A" dominates individual "B" and also all the birds that "B" dominates, and so on.

## Determining Foraging Niche of Natural Flocks

I defined a foraging site as a specific area at which an individual directed its attention for at least several seconds while in search of food. During these seconds, the bird exhibited certain behavior patterns associated with foraging, such as bill-probing, bark-flaking, and pecking. Actually discovering and utilizing a food item was not part of the definition of a foraging site. After identifying an individual, I estimated the height of the foraging site and also the height of the tree containing the site. Because the ground was covered with snow during most of the study, I restricted my observations to those foraging sites located in trees or shrubs. I recognized two types of foraging sites, the main trunk, or trunks, and the branches. The main trunk was either the vertical central axis of the tree or, in cases of multi-trunked trees or shrubs, the largest vertical appendages. If the foraging site was located on a branch, I determined the position of the site relative to the inner, middle, or outer third of the tree's canopy. I also estimated the diameter of the branch at which the bird was directing its foraging behavior. I made only five consecutive observations of an individual at one time.

All of the data gathered on foraging was first sorted by computer according to age and sex: adult male, juvenile male, adult female, or juvenile female. Birds whose wing length fell between the upper critical limit for females and the lower critical limit for males were disregarded in this analysis. I used the Student's t-Test to determine if the four age and sex groups differed in reference to the mean tree height, mean site height, and the mean branch diameter of foraging sites. With an F Test (variance ratio), I tested for differences in the variances of these three foraging-site parameters for the groups. I used a Chi-Square Test to determine relative differences in the number of branch-foraging versus trunk-foraging sites, and the number of branch-foraging sites in the three canopy positions, for the four age and sex classes of birds.

The computer then re-sorted all of the data according to the per cent of flock-mates over which each bird was dominant. This was determined by subtracting the bird's dominance position (i.e., 1 for alpha, 2 for beta, etc.) from the flock size and dividing that number by the number of flock-mates. I grouped data into four dominance classes based on the per cent of flock-mates dominated: 100–75, 74–50, 49–25, 24–0. The same statistical tests then were conducted on the foraging parameters for individuals within these classes.

## Breeding Success Data

During the breeding seasons of 1970 and 1971, I attempted to monitor the breeding success of those individuals remaining in the study area. I located nests and color-banded nestlings for as many breeding pairs as possible. During the summer of 1971, I endeavored to determine where breeding pairs foraged in the southern half of the study area, particularly during the late incubation and nestling phase of the breeding cycle. I plotted these locations on aerophotos and used a planimeter to determine the sizes of the foraging areas.

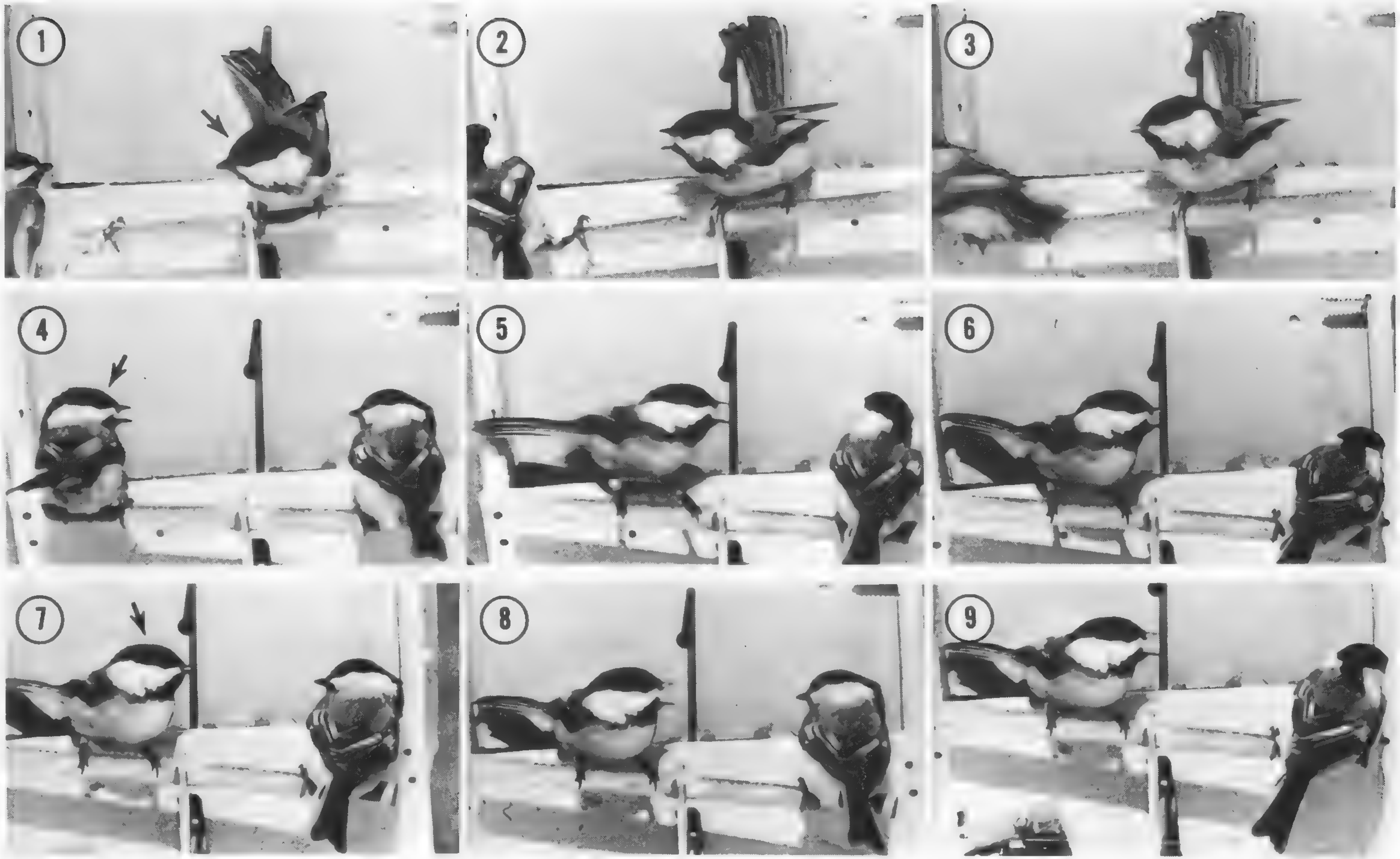

Figure 2. Sequences from three different agonistic interactions (1–3, 4–6, 7–9). In each interaction, the bird indicated by the arrows is threatening another bird, which responds with an appeasement display. In the threat display, note the raised crown and open bill. The display is always directed toward another bird. In the appeasement display, the feathers are compressed and the bill is closed; the head is turned and the body leans away from the threatening bird.

## *Formation of Flocks*

After a nestling period of about fifteen days, the young Black-capped Chickadees fledge and associate closely with the parents, which continue to feed their young. During this period the parents and their fledglings center their activities within the boundaries of the breeding territory, although they frequently trespass into the territories of neighboring birds.

Broods fledge from the second week of June to as late as the middle of July. The earliest breeding adults and their young comprise the earliest "family flocks." These data indicate that family flocks remain together for about two weeks, after which the young of each breeding pair begin to disperse, drifting away from their parents' territory and into the territories of neighboring chickadees. The longest period of association that I observed of a parent with one of its own young was 19 days after fledging.

In addition to the breeding pair and their young, I frequently saw other juveniles associating with family flocks. Since I knew the breeding activities of most of the adult birds in my study area and color-banded their nestlings, these unbanded young had entered the study area after traveling some distances from their nests. These "foreign" juveniles occasionally begged for food from the adult birds, but were either ignored or attacked. The presence of foreign juveniles was particularly evident in the family flocks of the late breeding adults. During the last two weeks in June of 1970 and 1971, none of the family flocks I observed had foreign juveniles associating with them. During the first two weeks of July, the flocks I observed had an average of 1.4 foreign juveniles per flock (SD = 0.9). These thirteen flocks were of two kinds: nine flocks resulted from the earliest breeding adults, whose young were starting to disperse, or shortly would do so, and four flocks resulted from later breeding adults whose young had just recently fledged.

Mid-season breeders and their associated young in the seven flocks I observed during the last two weeks of July of 1970 and 1971 averaged 3.7 foreign juveniles per flock (SD = 1.2). These flocks also contained a few of the banded juveniles from the earliest family flocks in my study area. However, with two exceptions, all 118 nestlings that I banded in my study area during these two seasons disappeared by the second week in August. All young found in the study area after this date were foreign juveniles. During August this represented about 4.5 juveniles per flock for the 16 flocks observed in that period (SD = 1.4).

During July and August of 1970 and 1971, I captured and banded 52 foreign juveniles in the southern third of my study area as shortly after their arrival as possible. Twenty of these disappeared. The others restricted their activities to definite areas and usually associated with one of the breeding pairs in that area. Because of the inevitable time lag between the initial arrival of a juvenile and its capture, I could not determine whether the foreign juveniles associating with a particular family flock before being captured were the same birds that later became permanent members of the winter flock in that area. However, with the exception of the disappearance of certain individuals in late August and early September, the composition of the flocks found in mid-August remained constant throughout the rest of the flocking period.

## *Composition of Flocks*

Based on an analysis of 23 flocks in the fall, the mean flock size was 6.35 (SD = 1.61). There were two flocks with four birds, one with five, eight with six, ten with seven, and one each with eight and nine birds. Each flock averaged 2.56 males, 2.61 females, and 1.18 birds of unknown sex (Figure 3).

In the 16 flocks for which I determined the age of all flock mates, 45.4 per cent were adults and 54.6 per cent were juveniles. Of the adults, 39.5 per cent were adult males that had previously bred in the flock's current territory, 27.9 per cent were females that had bred in the flock's territory, 16.3 per cent were non-breeding males, and 16.3 per cent non-breeding females. Thus, the average flock contained 1.06 adults as past breeding males, 0.81 females that formerly mated with these males, 0.38 non-breeding males, 0.44 non-breeding females of a former flock, and 3.57 juveniles.

## *Dominance-hierarchies within Flocks*

In determining the factors important in influencing the amount of dominance an individual attains within its natural flock, I relied heavily on observations of flock-mates interacting at feeders. To supplement this approach, I observed over 200 unambiguous interactions between individuals of six free-roaming flocks during the winter of 1971–1972. All of these interactions supported the flock-hierarchy structures I had determined by observing interactions at feeders. The outcome of encounters between flock-mates was completely unilateral with one individual always either dominant or subordinate to another. The individuals within a flock-hierarchy could be ranked in a linear arrangement, there being no triangular dominance relationships in natural flocks.

For birds whose sex had been determined on the basis of breeding behavior, males always dominated females. This category included 17 males and 13 females, all of which had bred in the study area at some time. Using wing length for predicting the sex of juveniles and non-breeding adults (see Appendix I), I found that males almost always dominated females. The only exception was Flock 22, where a female dominated a male. Thus, of the 59 males in the 23 flocks, 58 dominated all females in their respective flocks.

Of the birds classified as males, adults always dominate juveniles. Birds classified as adult females dominated juvenile females, with two exceptions: Flock 18, two juvenile females dominated an adult female.

The adult males that had bred within the flock's winter range were always the most dominant birds in the flock. The previous mates of these males were always the most dominant females. If more than two pairs had bred within the flock's winter range (Flocks 3 and 8), the pair with the largest and most centrally located breeding territory, relative to the winter range, became the most dominant individuals within their sex class in the flock.

Within a sex and age group, body size did not seem to correlate with hierarchial position. The more dominant juveniles of both sexes were not necessarily the largest within their sex class. This was tested statistically by using the Sign Test. The results from the 19 paired comparisons yielded 11 larger juveniles dominating smaller ones, and eight smaller juveniles dominating larger flock-mates. The probability that this differs from a 1:1 ratio is 0.64, a non-significant difference.

Dominance-relationships once formed are rigidly adhered to. I observed no change in the structure of the hierarchy throughout the season. The dominance relationships of those individuals that remained in the study area for more than one flocking period remained stable with two exceptions: in both Flocks 12 and 16, the female that paired and bred with the alpha male became the most dominant female in the next season's flock, dominating a female to which each had previously been subordinate.

## *Behavior of Natural Flocks*

Winter flocks restricted their movements to an area which the males, particularly the adult male that had bred in the area, defended against encroachment by neighboring flocks. During the winter of 1970–1971, I observed over 76 inter-flock territorial disputes. In the majority of these, the alpha male of the home flock was the most actively aggressive bird; but in 19 definite instances, I observed lower ranking males in the home flock chasing intruding birds away. Chickadee flocks were very opportunistic about entering the territories of neighboring flocks. Inter-flock encounters occurred at the rate of 1.5 per hour for 20 hours of observations made in January and February, 1972.

After entering the territory of a neighboring flock, the intruding flock appeared to give the contact note much less frequently, although I did not collect data on this. They remained in the neighboring flock's territory for up to 30 minutes before returning to their own area; but frequently the home flock discovered them and forced the trespassers to leave more quickly. Usually, the alpha male and some of the other males flew to the site of the intrusion, scolding loudly. Many of the intruding flock members left immediately, often flying non-stop to their own area. Any individuals that did not immediately leave were repeatedly displaced from their perches by males of the home flock, which gave dominance notes and scolded loudly as they followed the intruders from one tree to the next. In this manner the remainder of the intruding flock was escorted to the common boundary. Usually during these flock encounters, the females of the home flock remained nearby and scolded, but never took a more active part in territorial defense. When two neighboring flocks met along a common boundary, long scolding bouts usually developed between them.

I usually found flocks in one of three to five favored foraging areas within their territories. These sites probably resulted from the generally clumped distribution of suitable foraging habitat, the nature of which varied seasonally. For example, during the fall, flocks spent considerable time feeding on the seed heads of goldenrods (*Solidago* sp) and other field annuals, but ignored these areas during the winter, spending most of their time gleaning woody plants for insect material.

While in one of its preferred foraging areas, a flock slowly moved in one direction for a while and then slowly drifted in another, frequently retracing its previous path. Foraging flocks remained fairly compact and individuals seemed to maintain either visual or auditory contact with their flock-mates. Very seldom did I find an individual so isolated from its flockmates that I was unable to hear the latter's contact notes. When this occurred, the separated individual usually appeared agitated, spending much time giving the *chickadee-dee-dee* vocalization, and shortly rejoined the

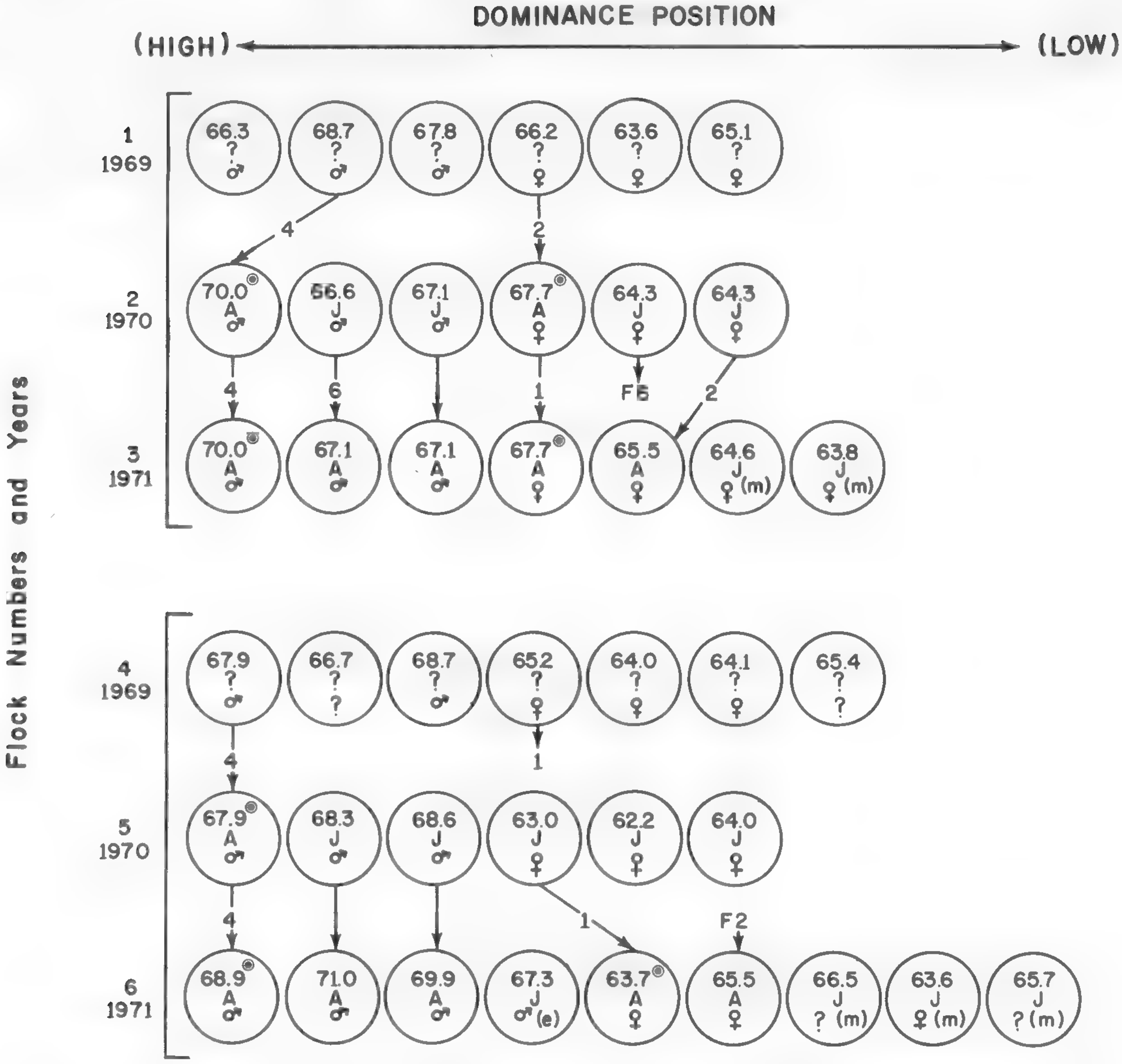
DOMINANCE POSITION
(HIGH)
(LOW)
Flock Numbers and Years
1 1969
66.3 ? ♂
68.7 ? ♂
67.8 ? ♂
66.2 ? ♀
63.6 ? ♀
65.1 ? ♀
4
2
2 1970
70.0 A ♂
56.6 J ♂
67.1 J ♂
67.7 A ♀
64.3 J ♀
64.3 J ♀
4
6
1
F6
2
3 1971
70.0 A ♂
67.1 A ♂
67.1 A ♂
67.7 A ♀
65.5 A ♀
64.6 J ♀ (m)
63.8 J ♀ (m)
4 1969
67.9 ? ♂
66.7 ? ?
68.7 ? ♂
65.2 ? ♀
64.0 ? ♀
64.1 ? ♀
65.4 ? ?
4
1
5 1970
67.9 A ♂
68.3 J ♂
68.6 J ♂
63.0 J ♀
62.2 J ♀
64.0 J ♀
4
1
F2
6 1971
68.9 A ♂
71.0 A ♂
69.9 A ♂
67.3 J ♂ (e)
63.7 A ♀
65.5 A ♀
66.5 J ? (m)
63.6 J ♀ (m)
65.7 J ? (m)

Figure 3. A summary of the history, dominance, sex, age, wing length, and condition of skull pneumatization for the individuals in all the study flocks of Black-capped Chickadees. All data reflect flock composition in the fall of the year. The number within each circle is the wing length in millimeters; A = adult; J = juvenile; a question mark in the center indicates age unknown; a question mark in the lower line indicates sex unknown; letters in parentheses indicate individual in early (e), middle (m), or late (l) pneumatization class. Other symbols indicate the following:

◉ = Individual bred in area occupied by previous winter flock.

$\overset{|}{\underset{\downarrow}{3}}$ = Individual bred in area with previous flock-mate in dominance position three.

↓ = Individual remained in area and did not breed.

┆↓ = Individual remained in area over summer, but breeding activities not known.

$\underset{\text{F6}}{\downarrow}$ = Individual did not breed; later moved to area occupied by Flock 6.

$\underset{\downarrow}{\text{F2}}$ = Individual left Flock 2 to move into area.

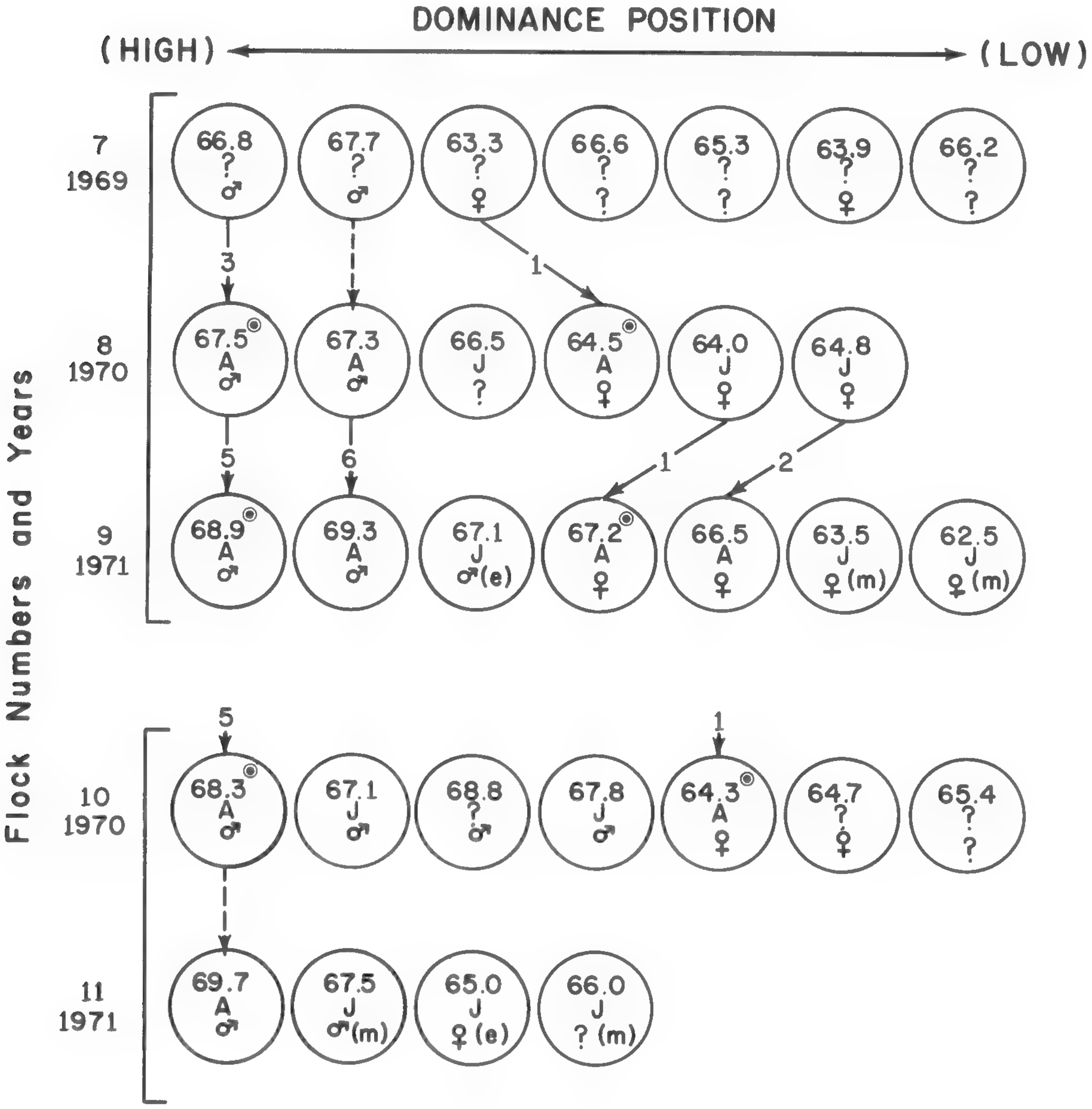
DOMINANCE POSITION
(HIGH)
(LOW)
Flock Numbers and Years
7
1969
66.8 ? ♂
67.7 ? ♂
63.3 ? ♀
66.6 ? ?
65.3 ? ?
63.9 ? ♀
66.2 ? ?
3
1
8
1970
67.5 A ♂
67.3 A ♂
66.5 J ?
64.5 A ♀
64.0 J ♀
64.8 J ♀
5
6
1
2
9
1971
68.9 A ♂
69.3 A ♂
67.1 J ♂(e)
67.2 A ♀
66.5 A ♀
63.5 J ♀(m)
62.5 J ♀(m)
5
1
10
1970
68.3 A ♂
67.1 J ♂
68.8 ? ♂
67.8 J ♂
64.3 A ♀
64.7 ? ♀
65.4 ? ?
11
1971
69.7 A ♂
67.5 J ♂(m)
65.0 J ♀(e)
66.0 J ? (m)

**Figure 3** (continued)

flock. These separations usually resulted when a bird remained in an area feeding on a large food item or an abundance of small items, while the rest of the flock moved rapidly to another area.

In naturally foraging flocks during the winter months, I observed about 3.0 aggressive interactions per hour. Almost all of these involved one individual displacing another from a foraging site, none of which were contested by the displaced bird.

## *Foraging Niches of Natural Flocks*

During the winter of 1971–1972, I selected five flocks (Numbers 13, 15, 17, 20, 22) for studying foraging niches. I have summarized their compositions, and past histories, in Figure 3 and their territories in Figure 4A. I banded all members of these flocks, determined the age and sex of most of them, and defined the flock-hierarchies prior to December 20, after which I maintained no feeders. During the months of January and February, I spent approximately 29 hours observing the foraging behavior of members of these flocks.

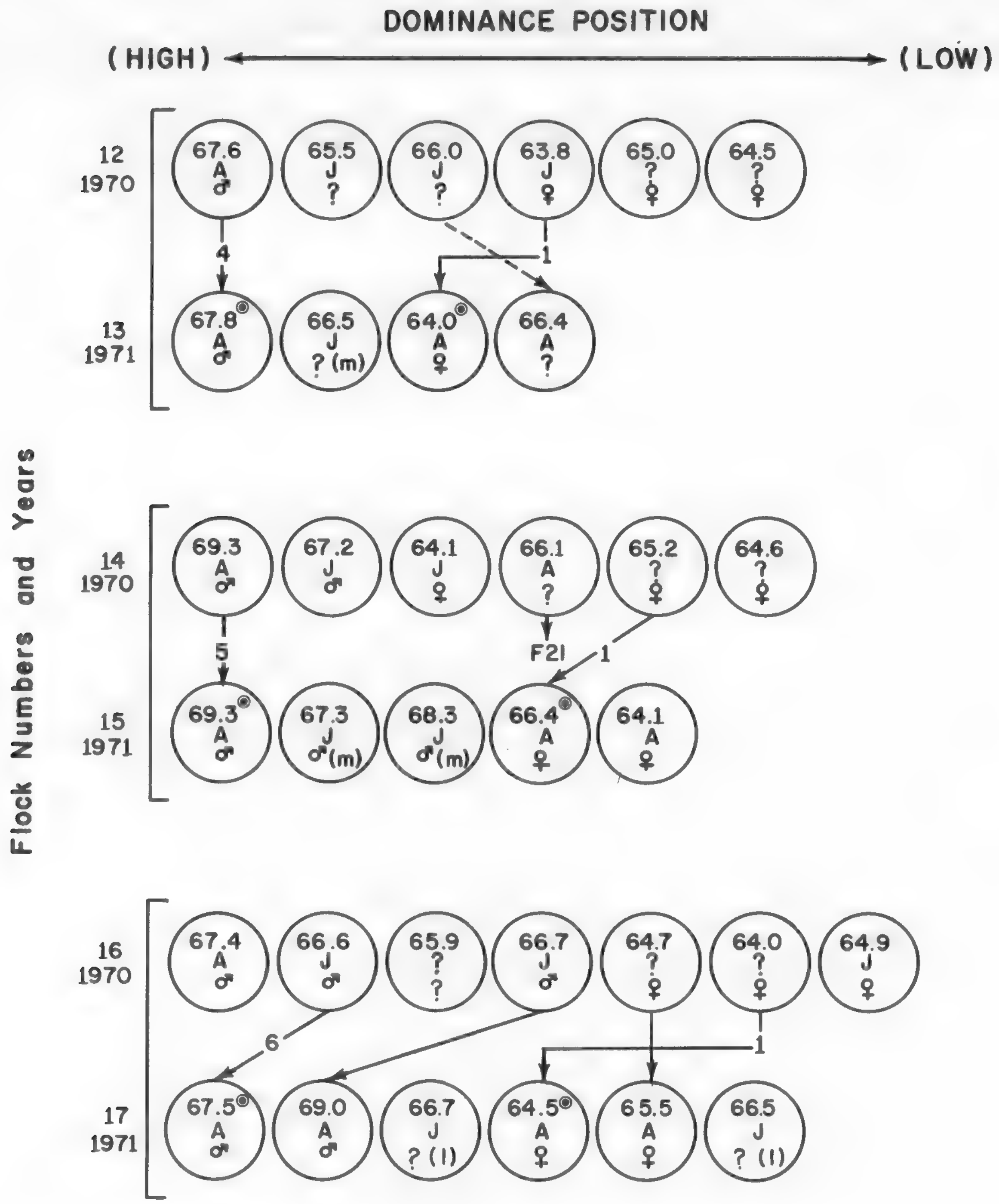
DOMINANCE POSITION
(HIGH)
(LOW)
Flock Numbers and Years
12
1970
67.6 A ♂
65.5 J ?
66.0 J ?
63.8 J ♀
65.0 ? ♀
64.5 ? ♀
4
1
13
1971
67.8 A ♂
66.5 J ? (m)
64.0 A ♀
66.4 A ?
14
1970
69.3 A ♂
67.2 J ♂
64.1 J ♀
66.1 A ?
65.2 ? ♀
64.6 ? ♀
5
F21
1
15
1971
69.3 A ♂
67.3 J ♂(m)
68.3 J ♂(m)
66.4 A ♀
64.1 A ♀
16
1970
67.4 A ♂
66.6 J ♂
65.9 ? ?
66.7 J ♂
64.7 ? ♀
64.0 ? ♀
64.9 J ♀
6
1
17
1971
67.5 A ♂
69.0 A ♂
66.7 J ? (l)
64.5 A ♀
65.5 A ♀
66.5 J ? (l)

Figure 3 (continued)

Dominance Class 1 contained only the adult males which bred the previous summer in the range of the winter flock. These males dominated all of the other birds within the flock. The birds of Dominance Class 2 dominated 50 to 74 per cent of the flock-mates, and consisted of all the juvenile males plus one adult male. Dominance Class 3 — the past mates of birds in Dominance Class 1 plus one other adult female — dominated 25 to 49 per cent of the flock-mates. Other adult females and juvenile females make up Dominance Class 4, dominating 1 to 24 per cent of other birds in the flock. I could not estimate, within the 0.95 level of confidence, the sex of three individuals in these flocks and, therefore, disregarded observations on these birds.

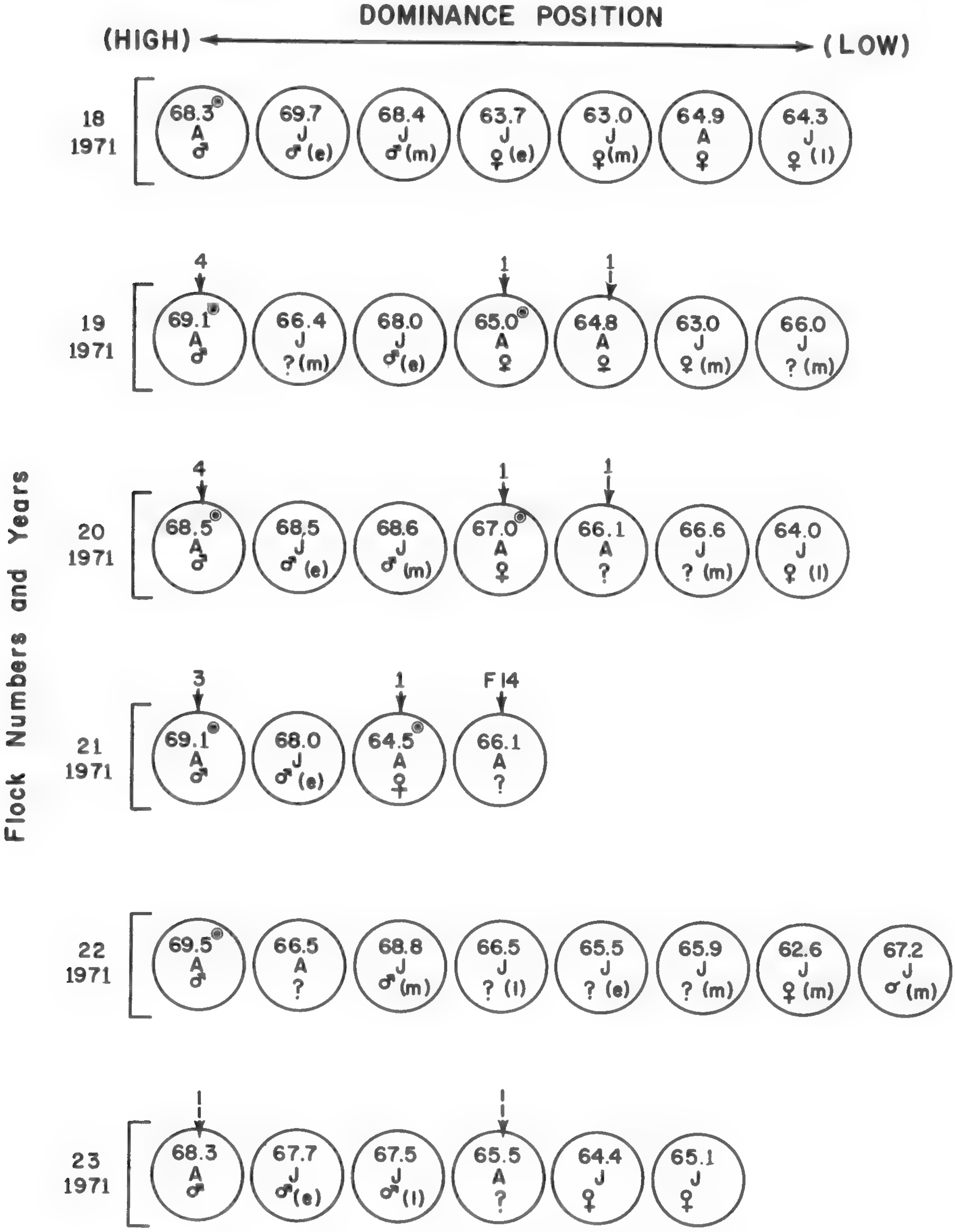
DOMINANCE POSITION
(HIGH)
(LOW)
Flock Numbers and Years
18 1971
68.3 A ♂
69.7 J ♂ (e)
68.4 J ♂ (m)
63.7 J ♀ (e)
63.0 J ♀ (m)
64.9 A ♀
64.3 J ♀ (l)
19 1971
4
1
1
69.1 A ♂
66.4 J ? (m)
68.0 J ♂ (e)
65.0 A ♀
64.8 A ♀
63.0 J ♀ (m)
66.0 J ? (m)
20 1971
4
1
1
68.5 A ♂
68.5 J ♂ (e)
68.6 J ♂ (m)
67.0 A ♀
66.1 A ?
66.6 J ? (m)
64.0 J ♀ (l)
21 1971
3
1
F14
69.1 A ♂
68.0 J ♂ (e)
64.5 A ♀
66.1 A ?
22 1971
69.5 A ♂
66.5 A ?
68.8 J ♂ (m)
66.5 J ? (l)
65.5 J ? (e)
65.9 J ? (m)
62.6 J ♀ (m)
67.2 J ♂ (m)
23 1971
68.3 A ♂
67.7 J ♂ (e)
67.5 J ♂ (l)
65.5 A ?
64.4 J ♀
65.1 J ♀

Figure 3 (continued)

Tables 1 through 5 show the results of the statistical analysis of the data grouped according to either age and sex or dominance class of the foraging bird. The parameters considered include: (1) height of the tree, (2) height of the foraging site, (3) diameter of the branch of the foraging site, (4) the numbers of foraging sites on trunks versus branches, and (5) the per cent of branch-foraging sites located in the inner, middle, and the outer parts of the canopy.

In summary, juvenile males differ from adult males only in their greater use of trunks as foraging sites. Adult females, although they forage at about the same height as males, differ from them in all other parameters considered, feeding in significantly shorter trees, on fewer trunks, and more frequently on smaller branches in the outer canopy. Juvenile females differ most: they differ significantly in all five foraging parameters compared to adult and juvenile males, and in four parameters compared to adult females. Thus, juvenile females forage in smaller trees, feed lower within these trees, forage infrequently on trunks, and spend more time foraging on smaller branches in the outer canopy of the tree. Males have significantly larger variances than females for the means of foraging-site height and branch diameter; adult males have a larger mean tree height variance than juvenile males.

Adult non-breeding and juvenile females forage in smaller trees, at lower sites, less frequently on trunks, and spend more time on smaller branches in the outer part of the canopy than other chickadees. Although adult past-breeding females forage in trees of the same height as males, they differ in all other parameters. Adult past-breeding males forage significantly higher than juvenile males but differ in no other parameters. Dominance Class 1 has a significantly larger mean variance of tree height than the other three classes. All four classes differ significantly for the variance of the mean height of foraging, the order from largest to smallest as follows: Class 1, Class 3, Class 2, Class 4. The variances for mean diameter of branch site are the same for Class 1 versus 2 and for Class 1 versus 3, but different for Class 2 versus 3 and for Classes 1, 2, and 3 versus 4. Class 4 has the smallest variance for this parameter.

The data also allowed a comparison of the foraging activities of adult, past-breeding females in the flock's current territory with adult, non-breeding females. Past breeding females forage significantly higher (7.80 m versus 5.55 m) and have foraging sites on larger branches (1.65 cm versus 1.19 cm) than the non-breeding females. They also forage on trunks more frequently (14.0 per cent versus 4.0 per cent) than non-breeding females. In addition, the variances for the mean tree height (27.67 versus 11.26; $F = 2.46$), the mean foraging-site height (23.70 versus 4.73; $F = 5.01$), and the mean branch diameter (1.74 versus 0.84; $F = 2.07$) are all significantly greater for the past-breeding females in the area.

During the 29 hours actually spent watching the five flocks forage, I observed 91 dominance interactions and identified both the participants and the outcome of 64 of these encounters. Twenty-nine interactions occurred between two females, 21 involved two males, and 14 involved a male and a female. The five flocks studied contained 22 birds of known sex, 10 males and 12 females. Assuming that the probability of any two birds interacting is unrelated to the sex of the birds, then in 64 interactions about 32 will be inter-sexual and 32 intra-sexual. The observed ratio was 50:14, which, if tested, indicates a highly significant difference between the two ratios (alpha less than .005).

On 28 February 1972 I spent one hour with each of two flocks and observed 18 agonistic interactions. Local environmental conditions that day probably caused this high level of aggression. A storm the previous night covered all tree surfaces with a thick coating of ice, drastically limiting the foraging sites available for chickadees. The majority of the displacements involved higher ranking birds displacing lower ranking birds of the same sex, although I observed five clear cases of inter-sexual displacements.

## *Dominance-hierarchies between Flocks*

Flocks defended their foraging areas against encroachment by chickadees of other flocks. However, if I maintained a feeder for an extended period within a flock's territory, neighboring flocks eventually gained uncontested access to the feeder. Initially, the resident males acted aggressively toward visitors attempting to use the feeder, but eventually the resident birds tolerated other chickadees in the vicinity of the feeder. Over a long period of time, a large feeding aggregation built up, composed of resident birds and individuals from nearby flocks. Adjacent flocks nearest to the feeder generally joined the home flock first in use of the feeder. Flocks located farther from the feeder — up to 1.25 km away — became members of the feeding aggregation later.

Within age and sex classes, the resident flock-members usually dominated individuals at the feeder. The resident alpha male dominated all other birds visiting the feeder. The resident flock's most dominant female dominated all visiting identifiable females with which she interacted, as well as a few males (0.95 probability). The resident juvenile males dominated visiting juveniles in the feeding aggregation. In the three home

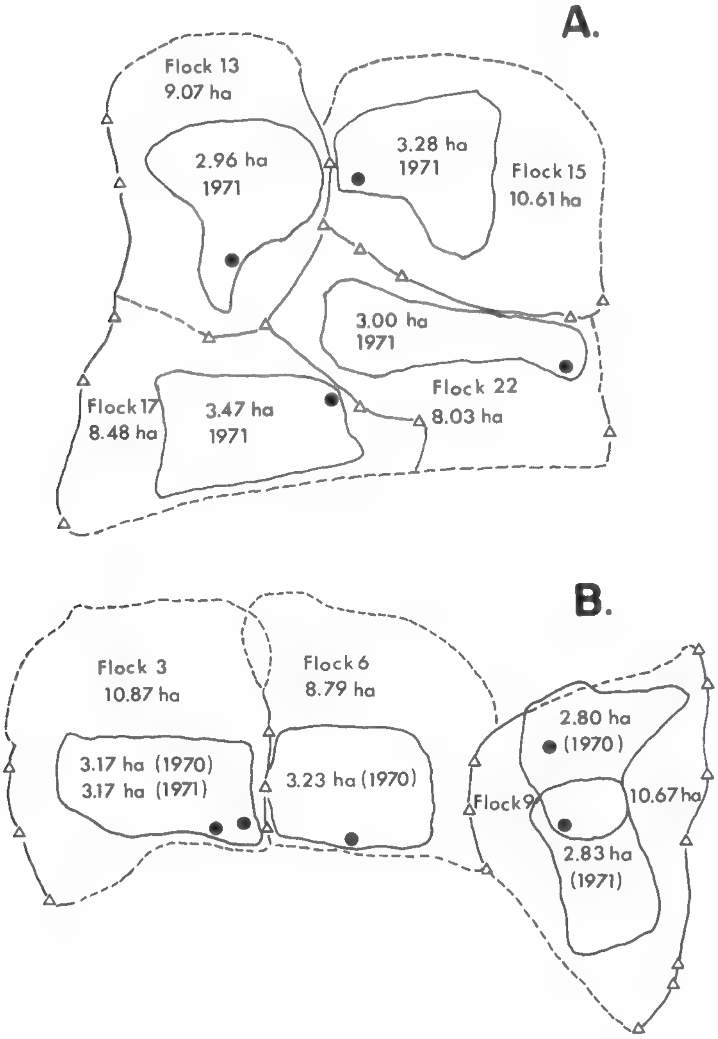
A.
Flock 13
9.07 ha
2.96 ha
1971
3.28 ha
1971
Flock 15
10.61 ha
3.00 ha
1971
Flock 22
8.03 ha
Flock 17
8.48 ha
3.47 ha
1971
B.
Flock 3
10.87 ha
Flock 6
8.79 ha
3.17 ha (1970)
3.17 ha (1971)
3.23 ha (1970)
2.80 ha
(1970)
Flock 9
10.67 ha
2.83 ha
(1971)

Figure 4. A comparison of the foraging area (in hectares) of the alpha pair of Black-capped Chickadees during the breeding season (smaller areas) with the territory of the flock dominated by each alpha pair during the following winter (larger areas). Δ = sites of territorial encounters between flocks during fall and winter. • = nest sites.

## TABLE 1

Relationship between the Height of the Tree Containing the Foraging Site and the Age, Sex, and Dominance of Foraging Birds

| *Age and sex class* | *Sample size* | *Mean height** | *Standard deviation* | *Dominance class* | *Sample size* | *Mean height** | *Standard deviation* |
|---|---|---|---|---|---|---|---|
| (1) Adult males | 165 | 11.86 | 6.83 | (1) .75–1.00 | 157 | 11.83 | 6.89 |
| (2) Juv. males | 145 | 12.34 | 4.91 | (2) .50– .74 | 224 | 11.09 | 5.00 |
| (3) Adult females | 291 | 10.64 | 4.72 | (3) .25– .49 | 184 | 11.31 | 5.46 |
| (4) Juv. females | 230 | 9.27 | 6.10 | (4) .00– .24 | 271 | 9.60 | 5.36 |

| *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* | *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* |
|---|---|---|---|---|---|
| (1) versus (2) | –0.69 | 1.93** | (1) versus (2) | 1.20 | 1.81** |
| (1) versus (3) | 2.28** | 2.09** | (1) versus (3) | 0.76 | 1.59** |
| (1) versus (4) | 4.00** | 1.25** | (1) versus (4) | 3.69** | 1.64** |
| (2) versus (3) | 3.50** | 1.08 | (2) versus (3) | –0.44 | 0.88 |
| (2) versus (4) | 5.11** | 0.65** | (2) versus (4) | 3.10** | 0.90 |
| (3) versus (4) | 2.90** | 0.60** | (3) versus (4) | 3.29** | 1.06 |

*Height in meters.
**Statistically significant at or above the .95 level of confidence.

flocks in which I knew the age of the birds, the five resident juvenile males dominated five of the seven visiting juvenile males. However, the alpha male from Flock 16, a juvenile, dominated all the juvenile males in Flock 5, and the most dominant juvenile male in Flock 10 dominated the second ranking male in Flock 2. The most dominant juvenile males in resident Flocks 2 and 8 dominated several visiting adult males. In general, however, adults dominated juveniles in feeding aggregations. Because females interacted less at feeders than males, the relationship of resident and home flock females was less clear. However, the highest ranking juvenile female dominated all visiting juvenile females with which she interacted.

The dominance relationships of the flock-mates in visiting groups known to be natural flocks (Flocks 7, 9, 10, 12, 14, and 16), and the relationships of the home flock members were all unilateral (A always dominates B), and the hierarchies for these flocks completely linear. However, when examining the dominance-relationships of the non-flock members in feeding aggregations, I found the existence of fairly numerous non-unilateral, ambiguous relationships. Also, dominance-hierarchies based on the unambiguous relationships of members in feeding aggregations were decidedly non-linear, because of the existence of triangular dominance-relationships.

During the two years of study of feeding aggregations, I observed 187 different non-unilateral (A dominates B as frequently as B dominates A) dominance-relationships. Slightly more than 70 per cent of the ambiguous relationships seen at a feeder during a two- to three-day period involved an older member of the feeding aggregation and a recently banded bird. For example, during mid-January, 1971, at the north feeder, six of the eight ambiguous relationships involved one of five recently banded birds and an older member of the aggregation. The ambiguous relationships seemed transitory and involved mostly new arrivals and older members of the feeding aggregations.

## *Dominance-Triangles*

Almost all the triangular relationships observed involved at least one recently banded bird and older members of the feeding aggregation. Like ambiguous relationships, dominance-triangles were also transitory, being resolved, where data was available, by the next observation period. For example, during several days of observations at the end of January in a feeding aggregation of 34 individuals at the south feeder, I discerned twelve triangular dominance-relationships. Fifteen individuals were involved in these triangles, of which eight had recently been banded (five males, two females, one of unknown sex) and seven were older members of the feeding aggregation (six males and one female). On 16, 17, and 18 February, all of these triangles had been resolved and three new ones were found among seven recently banded birds and two older members. In general, the dominance-positions of new arrivals were improved by the next observation period. Most of the dominance-triangles were resolved when a new arrival later became dominant to an individual to which it had previously been subordinate.

### Summary of Dominance Hierarchies

The dominance hierarchies found in natural flocks of Black-capped Chickadees are characterized by unilateral relationships among the flock-mates and a linear hierarchy. These relationships are stable wherever the flock goes. Even when the flock leaves its territory to encroach on the territory of a neighboring flock, the relationships remain stable. Thus, the outcome of encounters between flock-mates are not site-dependent, but absolute. The dominance-hierarchies for feeding aggregations of several different flocks are characterized by significant numbers of non-unilateral relationships and dominance-triangles, causing the hierarchy to be decidedly non-linear. The outcome of interactions between members of different flocks was site-dependent, with members of a flock being most dominant at feeders located in their territory.

An interesting natural analogue to the feeding aggregation of several flocks congregating at an artificial feeder occurred during the winter of 1971–1972. Flock 22 regularly fed on a white-tailed deer (*Odocoileus virginianus*) carcass located within its territory from December through February. By late December, two neighboring flocks (13 and 20) frequently fed on it, as well. Observations at the carcass revealed the dominance of the resident alpha male to all other birds using the carcass. The one resident juvenile male dominated the three visiting juvenile males and all of the females, although he was subordinate to the two visiting apha males. The highest ranking female (the alpha male's previous mate) in the resident flock dominated all of the females with which she interacted. Because juvenile females used the carcass less frequently, I did not learn their relationships. I found a similar feeding aggregation in the territory of Flock 9 during late February, again feeding at a deer carcass.

## *Spring Activities*

By the end of March and in early April, the alpha male of each flock became increasingly aggressive toward the other males in the flock. Typically, while feeding quietly, he suddenly displaced a nearby male several times in rapid succession, giving the dominance-vocalization with increasing frequency during this period. Gradually, during the first two weeks of April, the flock members disperse, leaving the alpha male and his mate occupying the main part of the flock's winter territory. By the third week in April, all the alpha males and their mates were alone on their future breeding territories.

I found small groups of birds, composed of members of several different flocks and unbanded birds, in peripheral parts of old flocking territories at this time. The existence of numerous unbanded birds suggests a general movement of birds during this period. In the ten flocks for which data are available (Flocks 1, 2, 4, 5, 7, 8, 10, 12, 14, and 16), 47.5 per cent of the flock-mates disappeared during this period, the majority of which were low-ranking males and females.

Of the 32 birds that remained in the study area over the summer, 26 formed pair-bonds, all between old flock-mates. Nine of these 13 pairs consisted of alpha males and juvenile females. The remaining six individuals spent the summer as solitary birds, joining flocks the following fall. Thirty of the 32 birds joined flocks in the same area as the previous year. Of the

## TABLE 2

### Relationship between Height of Foraging Site and Age, Sex, and Dominance of Foraging Birds

| *Age and sex class* | *Sample size* | *Mean height** | *Standard deviation* | *Dominance class* | *Sample size* | *Mean height** | *Standard deviation* |
|---|---|---|---|---|---|---|---|
| (1) Adult males | 165 | 7.65 | 5.55 | (1) .75–1.00 | 157 | 7.56 | 5.61 |
| (2) Juv. males | 145 | 7.04 | 3.75 | (2) .50– .74 | 224 | 6.13 | 3.93 |
| (3) Adult females | 291 | 7.04 | 4.21 | (3) .25– .49 | 184 | 8.17 | 4.88 |
| (4) Juv. females | 230 | 5.18 | 4.18 | (4) .00– .24 | 271 | 5.52 | 3.44 |

| *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* | *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* |
|---|---|---|---|---|---|
| (1) versus (2) | 1.09 | 2.58** | (1) versus (2) | 2.93** | 2.03** |
| (1) versus (3) | 1.34 | 2.06** | (1) versus (3) | –1.08 | 1.33** |
| (1) versus (4) | 5.06** | 2.08** | (1) versus (4) | 4.65** | 2.66** |
| (2) versus (3) | 0.05 | 0.80** | (2) versus (3) | –4.70** | 0.66** |
| (2) versus (4) | 4.40** | 0.81** | (2) versus (4) | 1.18** | 1.31** |
| (3) versus (4) | 5.03** | 1.01 | (3) versus (4) | 6.80** | 2.00** |

*Height in meters.
**Statistically significant at or above the .95 level of confidence.

### TABLE 3

Relationship between Branch Diameter of Foraging Site and Age, Sex, and Dominance of Foraging Birds

| *Age and sex class* | *Sample size* | *Mean diameter** | *Standard deviation* | *Dominance class* | *Sample size* | *Mean diameter** | *Standard deviation* |
|---|---|---|---|---|---|---|---|
| (1) Adult males | 74 | 2.41 | 1.50 | (1) .75–1.00 | 70 | 2.31 | 1.52 |
| (2) Juv. males | 51 | 2.64 | 1.88 | (2) .50– .74 | 91 | 2.54 | 1.70 |
| (3) Adult females | 263 | 1.47 | 1.22 | (3) .25– .49 | 156 | 1.75 | 1.37 |
| (4) Juv. females | 177 | 1.27 | 1.32 | (4) .00– .24 | 253 | 1.09 | 1.04 |

| *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* | *Comparison* | *Score of t-Test on means* | *Score of F-test on variances* |
|---|---|---|---|---|---|
| (1) versus (2) | –0.70 | 0.65 | (1) versus (2) | –0.79 | 0.79 |
| (1) versus (3) | 5.50** | 1.56** | (1) versus (3) | 2.85** | 1.24 |
| (1) versus (4) | 6.04** | 1.35** | (1) versus (4) | 7.79** | 2.11** |
| (2) versus (3) | 5.55** | 2.40** | (2) versus (3) | 3.96** | 1.55** |
| (2) versus (4) | 5.86** | 2.08** | (2) versus (4) | 9.31** | 2.68** |
| (3) versus (4) | 1.73** | 0.87 | (3) versus (4) | 5.37** | 1.73** |

*Measured in centimeters.
**Statistically significant at or above the .95 level of confidence.

six solitary individuals, two females moved to new areas and became members of the flocks that later formed there.

All of the alpha pairs successfully reared young. In the spring, three alpha pairs, for which I have data, initially defended almost all of the territory of the previous winter, each male trying to keep his previous flockmates from entering this area. After excavation of the nest hole was started, each pair began to spend much more time in the vicinity of the nest, and less in territorial defense. Figure 4 shows the relationship between the main foraging areas used by the alpha pairs during the incubation and nestling phases of the breeding cycle and the winter territory later defended by the flock the pair joined. I plotted the areas where each alpha pair foraged, and determined the flock's territorial boundaries by noting the location and results of agonistic encounters between flocks ("△" in Figure 4). The mean size of the alpha pairs' foraging area was 3.10 hectares (standard deviation 0.66) and the mean size of flock territories was 9.50 hectares (SD = 1.09). Thus, the alpha pairs foraged in an area that measured 32.7 per cent of the territory size of the flock in which they were later the most dominant individuals of their sex class. Odum (1941b) found that the winter flock's home range averaged 14.6 hectares.

Each alpha pair laid a mean clutch of 6.25 eggs; all eggs hatched and all young fledged. The mean hatching date was 8 June. Of the four pairs of second-ranking males and their mates, three pairs bred successfully. One pair replaced the alpha male and his mate from Flock 1 after both disappeared in mid-May. The other two pairs occupied small territories on the periphery of the territory of the previous alpha male and had an average clutch size of 4.67 eggs, with a mean hatching date of 22 June. The remaining pair maintained a small territory but made no attempt to breed. Two of these beta-pair territories were in areas which the alpha male had defended earlier in the season; but as he spent more time in the vicinity of his future nest, the beta pairs moved into these areas and became territorial.

## *Group Territoriality*

My observations that the average size of chickadee flocks varies little from six or seven birds agree well with several other studies on *Parus atricapillus* (Hartzler, 1970; Wallace, 1941; Whittle, 1926; Whittle and Fletcher, 1924). Butts (1931), Hamerstrom (1942), and Odum (1942) felt that larger flocks were common, but none clearly distinguished between natural groups and aggregations around artificial feeders. My findings that flock composition remained constant throughout the flocking period agree with studies made by Dixon (1963, 1965) on the Carolina and Mountain Chickadees. Hartzler (1970), working on *P. atricapillus,* arrived at the same conclusion independently of my study.

Dixon and Hartzler were reluctant to call the defended area a group territory because both observed that only the most dominant individuals actively defended a territory. I also found that the most dominant males participated most actively in territorial defense. However, since at some point most males actively defended territorial boundaries, and females became vocally active during periods of encroachment by neighboring flocks, I feel it is appropriate to use the term "group territory." Whatever the phenomenon is called, the result is the same — the reservation of an area used predominantly by members of a group.

### *Peck-right and Peck-dominance Hierarchies*

One important characteristic of a peck-right heirarchy is that there be no non-unilateral dominance-relationships. These can arise in two basically different ways. First, individuals can be actively competing for dominance status, such that A dominates B sometimes, but is dominated by B at other times, irrespective of the location of the encounter. The second type of non-unilateral dominance-relationship is site dependent, such that A dominates B in one area, but is subordinate to B in another area. Brian (1949) first described this type of relationship in her study of the Great Tit (*Parus major*). It involved an aggregation of birds at an artificial feeder and not a true flock, since the breeding pairs were territorial at this time. It is hard to conceive of an effective site-dependent dominance-hierarchy within a natural group. That none has been described led Dixon (1965) to suggest that the idea of peck-dominance as a principle of organization within a natural group be dropped.

My study of natural flocks revealed the complete absence of non-unilateral dominance-relationships of either type, even for those relationships that could be discerned during early flock-formation. I thus concur with Dixon's (1965) suggestion.

In all of the natural flock-hierarchies that I studied, I found no triangular dominance-relationships. This made the structure of the hierarchies completely linear, the second characteristic of a peck-right hierarchy. It is curious that there are no triangular relationships between members of natural flocks, because a hierarchy with a maximum number of triangles would be as stable as a hierarchy with none, providing that all of the relationships within the triangle were unilateral. Indeed, one would predict a very low probability that a group of seven individuals (21 unique dominance-relationships) will interact in such a way as to develop a completely linear hierarchy. Why should A, if dominant to B, also dominate all of the individuals that B dominates, and all of the individuals that these individuals dominate? That linear hierarchies have been found in field studies of natural groups argues for the existence of strongly adhered-to conventions governing the competition for dominance status. I use the term "convention" here in the manner first elaborated by Wynne-Edwards (1962) as an innate set of "rules" or "laws" governing the competitive behavior of animals.

The situation found in aggregations of flocks at feeders is more complex. Individuals of resident flocks dominate most visitors of similar age and sex. The alpha male dominates all birds at the feeder; resident juvenile males dominate visiting juvenile males and all females; the resident alpha male's previous mate dominates all females, etc. However, when the resident flock moves into the territory of a neighboring flock, it loses its competitive edge. Thus, in a feeding aggregation of several flocks, inter-flock hierarchies fit Allee's (1942) concept of peck-dominance while intra-flock hierarchies are of the peck-right type. The type of non-unilateral relationship resulting when individuals compete for dominance-status at one point in space was common in feeding aggregations. This type of relationship, and also triangular relationships, probably are simply temporary phenomena resulting from attempts to impose a hierarchial structure on a group of individuals still competing for dominance status. Since most of the ambiguous relationships and triangles involved a recent arrival at the feeder and

## TABLE 4

### Comparison of the Number of Foraging Sites on Trunks Versus Branches with Age, Sex, and Dominance of Foraging Birds

| *Age and sex class* | *Sites on trunks (per cent)* | *Sites on branches (per cent)* | *Dominance class* | *Sites on trunks (per cent)* | *Sites on branches (per cent)* |
|---|---|---|---|---|---|
| (1) Adult males | 55 | 45 | (1) .75–1.00 | 55 | 45 |
| (2) Juv. males | 65 | 35 | (2) .50– .74 | 59 | 41 |
| (3) Adult females | 10 | 90 | (3) .25– .49 | 15 | 85 |
| (4) Juv. females | 23 | 77 | (4) .00– .24 | 6 | 94 |

| *Comparison* | *Chi-square score (d.f. = 1)* | *Comparison* | *Chi-square score (d.f. = 1)* |
|---|---|---|---|
| (1) versus (2) | 3.00 | (1) versus (2) | 0.65 |
| (1) versus (3) | 113.18* | (1) versus (3) | 61.24* |
| (1) versus (4) | 41.87* | (1) versus (4) | 127.72* |
| (2) versus (3) | 146.36* | (2) versus (3) | 83.19* |
| (2) versus (4) | 64.13* | (2) versus (4) | 161.94* |
| (3) versus (4) | 18.40* | (3) versus (4) | 8.87* |

*Statistically significant at or above the .95 level of confidence.

### TABLE 5

### Comparison of the Location of the Branch-foraging Sites with Age, Sex, and Dominance of Foraging Birds

| *Age and sex class* | *Sample size* | *Percentage of foraging sites* | | | *Dominance class* | *Sample size* | *Percentage of foraging sites* | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *Inner canopy* | *Middle canopy* | *Outer canopy* | | | *Inner canopy* | *Middle canopy* | *Outer canopy* |
| (1) Adult males | 74 | 28.4 | 50.0 | 21.6 | (1) .75–1.00 | 70 | 31.4 | 45.7 | 22.9 |
| (2) Juv. males | 51 | 51.0 | 25.5 | 23.5 | (2) .50– .74 | 91 | 39.6 | 44.0 | 16.4 |
| (3) Adult females | 263 | 14.8 | 46.4 | 38.8 | (3) .25– .49 | 156 | 17.9 | 39.1 | 43.0 |
| (4) Juv. females | 177 | 17.5 | 39.5 | 42.9 | (4) .00– .24 | 253 | 12.2 | 43.2 | 44.6 |

| *Comparison* | *Chi-square score (d.f. = 1)* | *Comparison* | *Chi-square score (d.f. = 1)* |
|---|---|---|---|
| (1) versus (2) | 8.69* | (1) versus (2) | 1.59 |
| (1) versus (3) | 10.97* | (1) versus (3) | 9.79* |
| (1) versus (4) | 10.78* | (1) versus (4) | 18.90* |
| (2) versus (3) | 34.05* | (2) versus (3) | 22.82* |
| (2) versus (4) | 23.75* | (2) versus (4) | 39.92* |
| (3) versus (4) | 2.07 | (3) versus (4) | 2.60 |

*Statistically significant at or above the .95 level of confidence.

older members and were resolved by the new arrival attaining a higher position in the aggregation hierarchy, it seems reasonable that these transient relationships result as new arrivals are establishing their position in the hierarchy. Numerous studies (Braddock, 1949; Guhl and Allee, 1944; Sabine, 1959) have demonstrated, for a number of different species, that the newcomer is frequently at a disadvantage when interacting with older members of a group. Odum (1941a) transferred chickadees to a feeder in the home range of another flock and found that the introduced birds were relegated to the lowest dominance-positions without regard to previous positions held in their home flock. Eventually, some of these transferred birds became more dominant, ". . . apparently finding their proper level in the combined flock."

### *Factors Affecting Dominance*

As the number of individuals within a feeding aggregation increases, it must become more difficult for individuals to recognize which birds they dominate and to which they are subordinate. Because known males usually dominate known females, and assuming that chickadees can recognize morphological or behavioral differences in the sexes, the problem really becomes one of knowing only individuals within one's sex group. Males need only know other males, because they dominate all females, and females need avoid all birds looking or behaving like males, while learning individual females. Since adults usually dominate juveniles, a juvenile male only needs to known other juvenile males, avoid adult males, and expect subordination from females.

What might be the nature of the conventions governing competition for dominance status? The minor size dimorphism in chickadees makes it impossible to say that all males dominate all females. The largest females may dominate the smallest males, although this is unlikely since the most dominant female, the alpha male's previous mate, is always subordinate to her juvenile, male flock-mates. Also, no correlation exists between size and dominance status for birds of known sex. Numerous studies (Collias and Taber, 1951; Marler, 1955; Tordoff, 1954) show a general tendency for males to dominate females, although in some species females rank with their past or present mates (Brian, 1949; Jenkins, 1944; Lorenz, 1931). In his study of *Parus carolinensis*, Dixon (1963) felt that the dominance of the previous mate of the alpha male was enhanced when he was present, but reduced when he was elsewhere. I did not find this to be true with *P. atricapillus*. In most other species of Parids studied, males tended to dominate females (Hinde, 1952; Morley, 1943; Stokes, 1962a, 1962b). This general phenomenon may be related to the more aggressive nature of males, evidenced by their active defense of the flock's territory.

The general dominance of adult Black-capped Chickadees over juveniles suggests that prior occupancy of an area is an important underlying convention in determining the outcome of competition for dominance status. However, the dominance of juvenile males over adult females suggests that sex is a more important factor than age.

If size, as such, is unimportant, what determines the relationships of juveniles in the formation of flocks each August? Since Black-capped Chickadees have a rather extended breeding season, with eggs hatching from late May until early July, it seems reasonable that birds from early clutches might, on the average, reach the area in which they will join a flock sooner than juveniles from later clutches. These several extra weeks might allow the birds from earlier clutches to gain a more dominant rank in the flocks. Due to the time lag between a juvenile's arrival and its subsequent capture and color banding, I could not test this directly; but the results from my study of skulls (see Appendix I) indicate a positive correlation between the relative amount of cranial pneumatization by a particular date and the number of other juvenile flock-mates dominated. Although the confidence level of this correlation (0.92) is not acceptable at the standard level of significance, it suggests that the rank an individual attains in a flock-hierarchy is at least somewhat related to the degree of skull pneumatization. I believe it is an imperfect relationship for the following reasons: the amount of skull pneumatization at a particular date probably indicates only roughly the age of a juvenile (Nero, 1951; Serventy, *et al.*, 1967). A fair amount of variation probably exists between a chickadee's hatching date and its arrival in the winter flock area. Certainly, other factors also enter into the determination of the juvenile's dominance status, such as genetic contributions, and family-flock relationships.

Breeding success in a given area also was an important factor in determining the amount of dominance-status an individual attained. All of the alpha males were adults that had bred in the area which their winter flock occupied, and their previous mates now dominated all other females in the flock. It is revealing that in two cases the status of a female improved from one flock period to the next when she nested in the area during the intervening summer.

## *Effects on Foraging Activities*

One suggested function of a dominance-hierarchy (Wynne-Edwards, 1962) is the differential allocation of food resources, so that periods of food scarcity will reduce the chances of survival of only the lowest ranking individuals. However, the low levels of active aggression that I found within naturally foraging flocks suggests that either food is seldom limiting or that some means other than overt aggression implements the hierarchial structure. Some studies (Betts, 1955; Gibb, 1960) indicate that other titmice undergo a high winter mortality and greatly reduce population levels of certain prey species, suggesting that real food shortages occur. All the interactions I observed in naturally foraging flocks supported the dominance-hierarchies based on interactions at feeders, indicating the functioning of hierarchies within naturally foraging flocks.

The results from the foraging-niche study suggest two interrelated explanations of how hierarchies are implemented within chickadee flocks and how the birds maintain active aggression at such low levels. The marked differences in the foraging sites of males and females in reference to the five parameters considered (see page 247) could exist as a consequence of inter-sexual niche partitioning, or as the result of the competitive exclusion of females from certain foraging sites by the more dominant males. Numerous studies (Hoglund, 1964; Kilham, 1965; Selander, 1966; Storer, 1966; Ward, 1965) of species exhibiting secondary sexual dimorphism and inter-sexual niche partitioning generally support the hypothesis first articulated by Rand (1952) that, within a species, secondary sexual dimorphism may aid in reducing competition for food. In two studies of the essentially monomorphic Red-cockaded Woodpecker, *Dendrocopos borealis* (Ligon, 1968) and Downy Woodpecker, *Dendrocopos pubescens* (Jackson, 1970), the author found significant inter-sexual partitioning of foraging niches, indicating that behavioral foraging differences can exist independently of marked secondary sexual dimorphism.

The differences in foraging found within each sex probably represents competitive exclusion of the less dominant birds from certain foraging sites. For example, the different foraging sites of adult and juvenile males, adult and juvenile females, and particularly between the highest ranking adult female (previous mate of alpha male) and the other adult females, must be due to the greater access that more dominant individuals probably have to the better foraging sites. The statistically smaller variances for the mean birds of both sexes indicate that their foraging activities are more restricted than those of more dominant individuals. The fact that I observed significantly more intra-sexual aggressive encounters (78 per cent) than inter-sexual encounters (22 per cent) also indicates higher levels of competition between members of the same sex, and supports the idea of an inter-sexual partitioning of the foraging niche. This further suggests that the foraging activities of an individual may be affected most by its dominance-position relative to members of its own sex. Therefore, the dominance of males to females at feeders is of ecological significance only to the extent to which the sexes actively compete while foraging.

## *Effects on Breeding Success*

Less dominant individuals disperse from the study area in the spring. Only the alpha and beta males and their mates establish breeding territories within a winter flock's previous territory. Three times as many alpha males established territories as beta males. Dixon (1963) also found this to be true in his study of *P. carolinensis*, although he did not study reproductive success. In addition, alpha pairs laid larger clutches earlier than the three beta pairs that succeeded in breeding. Stefanski (1967) found that, although Black-capped Chickadees initially established an average territory size of 2.7 hectares in Utah during the period of nest-hole excavation, they actually used only 22 per cent of this area (0.7 hectares) during the nestling period. He found a 40 per cent reduction in the time birds spent in territorial defense from the excavation phase to the nestling stage. In addition, the territories of older males (six individuals) averaged 0.7 hectares larger than those of first year birds (three individuals), although Stefanski had no data on the previous dominance relationships of the individuals in his study. I did not attempt to measure directly the size of defended territory, but only the area used by pairs for foraging during the incubation and nestling phases. But in the three cases for which I have data, alpha males attempted to defend almost all the area that had been the flock's winter territory. Odum (1941b, 1942) reported an average territory size of 5.3 hectares for birds in eastern New York. This indicates that chickadees in this area establish considerably larger territories than the birds Stefanski studied in Utah, perhaps due to habitat differences. I found that during the incubation and nestling phase, the alpha pair used only about one-third of the territory they had originally established. My size estimates of foraging areas tend to be larger because I did not differentiate between the incubation and nestling phases while mapping foraging locations. The beta pairs established territories later in the season in those areas no longer used by the alpha pair. My data on dominance-relationships suggest that the first year birds in Stefanski's study were probably lower ranking males; and the fact that they had smaller territories agrees with my findings.

One would not expect the reproductive success of low ranking individuals that disperse from the study area in spring to be, on the average, as great as the more dominant individuals that remain in a familiar area to breed. The existence within the study area of several non-breeding adult birds seems to suggest that many of these individuals may become part of a general non-breeding adult population.

### *Evolution and Ecological Significance of Dominance-hierarchies*

In general, a Black-capped Chickadee flock can be viewed as a closed system after its establishment during August, remaining in a fixed, defended area until dissolution in April. If most bird populations are regulated in a density-dependent fashion outside of the breeding season, and if food is the most important limiting factor in this regulation, then high levels of competition for food in gregarious species should be common. That it is not poses a problem. In this regard, Wynne-Edwards' definition of society (1962:132) as ". . . an organization of individuals capable of providing conventional competition . . ." has much appeal. Direct, open, and continuous competition for food in the long run must end in over-exploitation and diminishing returns both for the individual and the social group. Wynne-Edwards feels that instead of competing directly for food, animals compete for that which will insure access to it, tenure of property, and status in a social group.

Individuals in a group actively competing for each food item, or favored foraging site, have to relegate a large portion of their energy budget toward aggressive behavior. This is probably impossible, particularly for small species living in areas with long cold winters. A dominance-hierarchy functions effectively because subordinate individuals accept their submissive roles; that is, they do not fight, or even threaten, a higher ranking individual that tries to assert its dominance. This acceptance is the intrinsic value of dominance. Individuals accepting a subordinate position after several defeats by another bird were probably favorably selected since losing out in future conflicts with that individual would result in wasted energy and time when both were at a premium. If lower ranking individuals accrue advantages from flock membership that outweigh the disadvantages of low dominance, then the evolution of dominance-hierarchies can be explained in Darwinian terms, without recourse to "group selection."

The greater aggressiveness of male chickadees, correlated with breeding and territorial defense, probably placed the females at a disadvantage when competing with the males during the flocking period. This could have led to the evolution of a small, but significant, separation of foraging niches between males and females. Ligon (1968) suggested that the general dominance of the male could have led to the niche partition he found in the monomorphic Red-cockaded Woodpecker. It is advantageous for some species to broaden their foraging niche by inter-sexual partitioning; but the mechanism by which this could be accomplished has not been clearly articulated. The clear dominance of one sex over another could lead to a niche partitioning based on the competitive edge that the more dominant sex has in using the optimum foraging sites. Natural selection would then favor those individuals better adapted to recognize and use the foraging sites available to them. This system would also be favored because of the resulting reduction in aggression between flock-mates.

In addition to exhibiting a social system based on dominance within flocks, a system of property tenure exists between different flocks. Suitable habitat is divided up into flock-territories during the non-breeding season, insuring that only a fixed number of individuals will have access to the food resources within a given area. The dominance-hierarchy insures that a certain number of these individuals will be maintained throughout the winter by placing the main brunt of food shortage on only the lowest ranking juveniles. These processes would selectively regulate the number of birds in relation to the levels of food resources in a given area and the existing weather conditions. Years of high winter mortality would leave potentially fewer reproductive individuals, but would maximize the possibility that birds previously successful at breeding would breed again.

## *Summary*

For three years I studied the social organization of 23 natural flocks of the Black-capped Chickadee (*Parus atricapillus*). Sex determination was based on a known size dimorphism. I estimated the area of unpneumatized skull for 44 juveniles and used a computer to analyze the inter- and intra-flock interactions recorded at feeders. During the last year, I studied the dominance hierarchies of five flocks that had no access to feeders, and characterized the foraging activities of birds of known age, sex, and dominance status according to five parameters of their foraging niche: height of the tree containing the foraging site, height of the site, number of trunk versus branch sites, and the diameter and location of branch foraging sites relative to the inner, middle, and outer canopy.

After formation in late summer, flock composition remained stable until the following spring. Within each flock, males dominated females; within sexes, adults dominated juveniles. There was a positive correlation ($P = 0.92$) between the degree of skull pneumatization by a particular date and the number of other juvenile flock-mates dominated, indicating that older juveniles attained higher dominance positions, possibly because they arrived earlier in the area where they wintered. The breeding pair that bred in the area the previous year were the most dominant. Male flock members defended an area that was an enlargement of the breeding territory of this pair. Intra-flock hierarchies were linear and unilateral, while the outcome of interactions between members of different flocks was site-dependent, with members of a flock being most dominant while in the flock's own territory.

The same hierarchies discerned at feeders were found effective in naturally foraging flocks, but the level of aggression was much lower. I also observed significantly ($P = 0.995$) greater intra-sexual (78 per cent) than inter-sexual (22 per cent) aggression.

The foraging niche study revealed significant differences in foraging correlated with age, sex, and dominance rank of the bird. The differences tended to be greater between sexes than between members of the same sex. Some differences could be correlated only with dominance rank. The most dominant adult females differed significantly in three niche parameters from lower ranking females. I suggest that the foraging differences between the sexes are due to an inter-sexual niche partitioning. Also, the higher levels of intra-sexual aggression and the size dimorphism argue for this. Inter-sexual foraging differences, I believe, result from the passive exclusion of the subordinate birds from the better foraging sites by the more dominant individuals. This system should allow adults of both sexes, particularly the previous breeding pairs, the greatest chance of surviving periods of low food availability.

## *Acknowledgments*

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# APPENDIX I

## Methods of Aging and Sexing Black-capped Chickadees

At the time of the study the only known external difference between male and female chickadees was a size dimorphism. I measured the wing length of 71 museum specimens of known sex and calculated the means and variances. With these data, I determined the probability that an individual with a known wing length was a male or female by testing (Student's t-Test) the mean wing length for known males and females against various wing lengths. Based on an analysis of 35 museum specimens of known males, the mean wing length was 67.26 mm (SD = 1.21). The Student's t-statistic indicated that a wing length of 67.1 mm or larger allowed a minimum probability of 0.95 that the bird was a male. Based on an analysis of 36 museum specimens of known females, the mean wing length was 65.02 mm (SD = 1.14). The Student's t-statistic indicated that a wing length of 65.1 mm, or smaller, allowed a minimum probability level of 0.95 that the bird was a female. Of the 145 birds in the 23 flocks, 40.7 per cent had wing length measurements that were 67.1 mm or greater, 41.4 per cent had wing length measurements that were 65.1 mm or smaller, and 17.9 per cent had intermediate wing lengths.

I supplemented this approach by observing the reproductive behavior of those individuals that stayed within the study area to breed. I considered a chickadee to be of a certain sex if its wing length fell within a .95 probability range for that sex, or if I observed some diagnostic reproductive behavior for the bird.

To age chickadees I made a small incision on the top of the head and determined the extent of air spaces, or pneumatization, in the cranium (Miller, 1946). I considered individuals with an incompletely pneumatized cranium as juveniles and those with a completely pneumatized cranium as adults. During the fall of 1971, I measured the unpneumatized cranial patches with a pair of dividers and made a scaled drawing of the cranium for each juvenile captured. Because of the extended period required to capture all the juveniles, I divided them into three groups: those aged during 1 November to 8 November, those aged during 9 November to 13 November, and those aged during 15 November to 1 December. I then calculated the area of the unpneumatized patch with a planimeter, and placed each juvenile in one of three size classes: Class 1 contained individuals with unpneumatized areas more than one standard deviation above the mean, Class 2 contained individuals with unpneumatized areas more than one standard deviation below the mean, Class 3 contained individuals with unpneumatized areas not greater or less than one standard deviation from the mean. I could not use cranial pneumatization to age birds after the second week in December, at which time the crania of some juveniles were identical to those of adults.

During December 1971, I determined the dominance relationships of the juvenile flock-mates of known age. I ran a Kruskal-Wallis one-way analysis of variance on the individuals in the three pneumatization classes ranked according to the number of other juvenile flock-mates that each juvenile dominated. My null hypothesis stated that there would be no significant difference in the number of other juvenile flock-mates dominated by birds from the three different classes.

I presumed that the relative degree of skull pneumatization that had been completed by a particular date would be a rough indicator of the age of juveniles. In using the Kruskal-Wallis analysis of variance to test for a correlation between pneumatization class and dominance status, the calculated value of H equals 5.18. This valuea llows a rejection of the null hypothesis at the 0.92 level of confidence.

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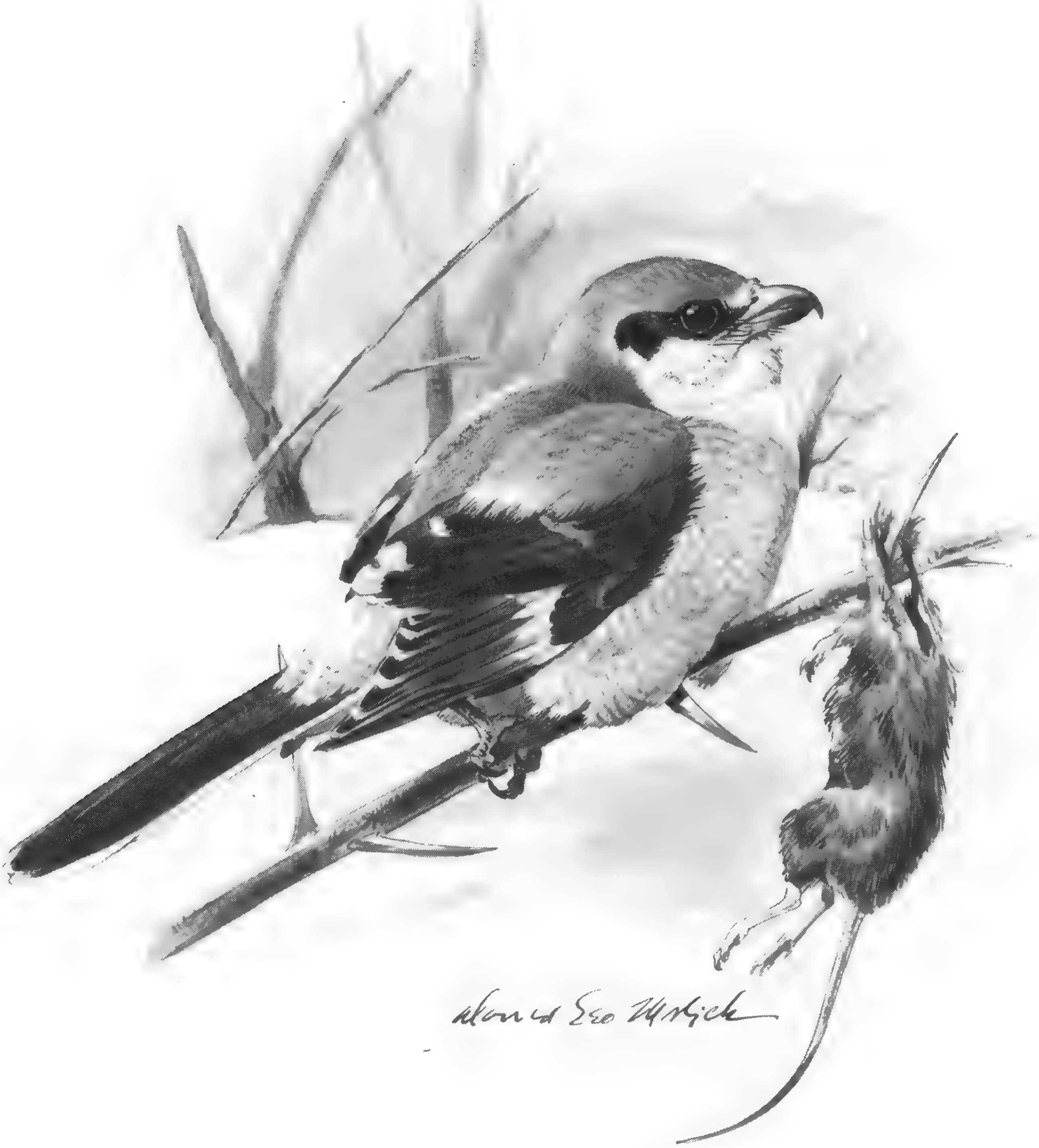

Northern Shrike, *Lanius excubitor*. Painting by Donald Leo Malick.

# AVIAN ECOLOGY OF A MANAGED GLACIAL MARSH[1]

MILTON W. WELLER AND LEIGH H. FREDRICKSON

The direct and vital role that vegetation plays in determining the use of an area by birds is most dramatically displayed in unstable habitats where birds have evolved adaptive responses to changing conditions. Although terrestrial systems change, the rate at which they do so is slow and measurement of bird adaptations difficult. Marshes, on the other hand, constantly undergo vegetative changes resulting from water fluctuations, which influence avian diversity and population size. In addition, habitat selection also becomes more obvious, as demonstrated by the observations of Beecher (1942) and Weller and Spatcher (1965).

In northern Iowa, as in other areas influenced by Pleistocene glaciation, there once were numerous shallow lakes and marshes rich in aquatic flora and fauna. Many of these lakes have been drained directly by ditches or indirectly by tilling of farmlands. However, acquisition of prime wetlands has been possible through the cooperative Federal-State Pittman-Robertson Program, which provides funds for acquisition of wildlife habitat, or through the refuge program of the Bureau of Sports Fisheries and Wildlife. Marshes so acquired often are maintained by water control structures, because natural drainage systems have been modified. Such control structures not only provide opportunity for marsh management but permit experimental studies of marsh succession and ecology which are less dependent upon rainfall. This paper reports observations made from 1964 to 1971 on an experimentally managed 400-acre marsh, Rush Lake, in Palo Alto County, Iowa. In this semipermanent marsh (Type IV of Stewart and Kantrud, 1971), we regulated water levels within the limits compatible with use of the area by hunters and trappers. Although there are other similar marsh areas within two and one-half miles, and two small adjacent "pothole" marshes, Rush Lake is a fairly discrete unit with its own water supply. Runoff into Rush Lake was high, both because of the topography of the area and the diversion of drainage water into the main inlet. Thus, siltation and turbidity were greater than in other similar marshes in northwest Iowa.

The major objectives of the study were (1) to record plant succession from the time of its establishment to its elimination by water and muskrats

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(*Ondatra zibethicus*), supplementing less complete observations on the natural changes on two glacial lakes in central Iowa (Weller and Spatcher, 1965); (2) to measure avian succession, diversity, and population fluctuations dependent on the plant substrate; (3) to clarify typical marsh habitat cycles to allow optional use of natural systems in management for marsh wildlife; (4) to experimentally lengthen the typical marsh habitat cycle to provide more uniform productivity of harvestable vertebrates over a longer period of time; and (5) to better describe the form and function of a discrete, natural ecosystem.

## *Methods*

### Chronology of the Draw-down

Because high water and muskrats had eliminated vegetation from Rush Lake during 1959 to 1962, a draw-down (lowering of water level) was employed to induce plant germination. This is a common technique among marsh managers (Kadlec, 1960). Water levels were lowered in the spring of 1963 but little germination occurred because of the large volume of water. A successful draw-down was achieved early in 1964 and levels were held low until the fall of 1964 (Figure 1).

Following successful germination of a great variety of moist-soil and aquatic plants, water levels were raised to flood the entire marsh bottom but only dampen the surviving cattail beds at the perimeters. In subsequent years, levels were varied between full pool (2.0 in Figure 1) and one to one and one-half feet below full pool, depending upon water supply and vegetative pattern. An attempt was made to flood openings in vegetation to a depth of one foot or more.

In 1971, another draw-down was conducted to regerminate the marsh. At this time, we measured populations of some nesting passerines not recorded during the draw-down of 1964.

### Appraisal of Vegetative Cover

Because of the size of the marsh, we considered impractical any attempt to quantify the composition or distribution of the vegetation of the entire lake. However, some aerial photographs and gross cover maps were made to facilitate field work (Figure 2). We prepared cover maps by pacing on ice in winter.

To more precisely map vegetative patterns and changes, and to sample both bird and muskrat populations, we selected belt-transects one hundred feet in width. One transect crossed the marsh in a generally north-south direction and traversed two shore zones, crossed the major water flow, and encompassed part of a large silt bred (Figure 2). The second and third transects also crossed the shore zones and met to form a right angle unit, sampling the marsh area less influenced by water movement (Figure 2).

More detailed indices to vegetative composition and dispersion, which also measured cover-water ratios and patterns, were permanent point-count transects along one edge of each belt transect. We recorded an emergent plant if within one inch of each foot-mark on the tape. Floating and submergent plants also were recorded at every foot, but two or more plants often were listed so that total plants tallied could exceed the number of points recorded by the tape. We recorded water depth at intervals of 25 feet or where dramatic changes were noted. We ran transcts annually following germination in 1964 through 1970 when the lake was open in the center and rimmed with a sparse stand of cattail.

### Appraisal of Bird Populations

We used three methods to evaluate changes in numbers of birds: (1) recording of nests found in the belt transects; (2) general observations of numbers of conspicuous birds, such as terns, grebes, ducks, and American Coot (*Fulica americana*); and (3) independent studies involving coots and terns, which included some observation of other species. In general, we emphasized abundant, marsh-restricted species which were easily found. Blackbird nest numbers were tallied in several years and recorded in the 1971 draw-down because we had not counted them in the draw-down of 1964.

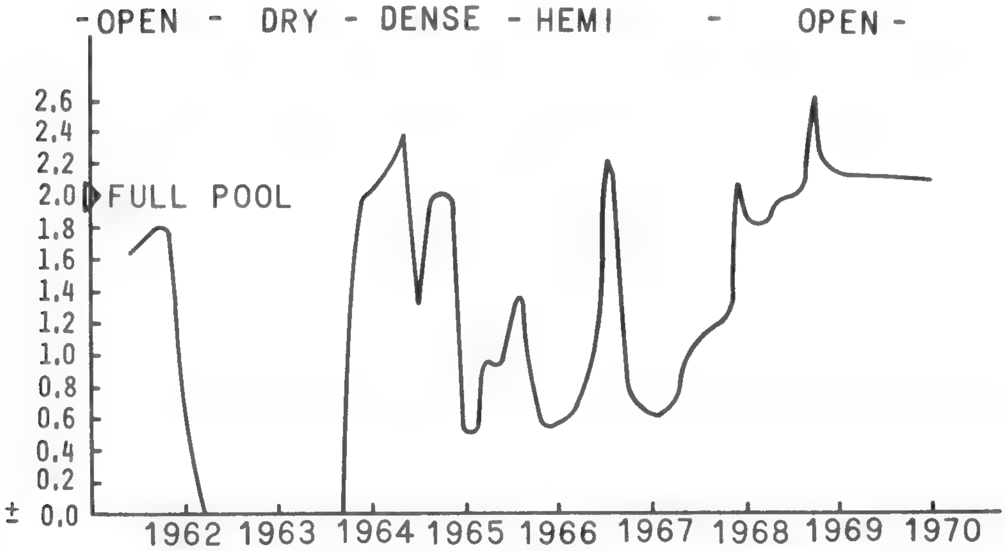


Figure 1. Water levels of Rush Lake, Palo Alto County, Iowa, 1962–1970.

The same belt-transects used to record vegetative patterns also were used for numbers and locations of nests of birds. Belts were searched by a crew of three to six persons, who waded through the vegetation and totaled nests found in each transect. In some years, we mapped belt transects to show the distribution and relationship of nests to open water.

Because these belts included 16 acres (4%) of the true marsh, general observations were very important in evaluating the accuracy of the sample. Fredrickson (1969; 1970; 1971) studied populations of the American Coot and Common Gallinule (*Gallinula chloropus*) in 1965 and 1966. Estimates of these populations for the entire marsh were more accurate for these years than for others. Several workers studied tern populations from 1966 through 1968 (Bergman, Swain, and Weller, 1970) and also recorded coots on much of the marsh. Because of these, and other, detailed studies, reasonably good estimates of bird numbers could be made for the entire marsh. In some cases, we based estimates on a factor of 20 to 25 times the numbers found in the 16 acres of the belt-transects, contingent upon the dryness and density of the west end of the marsh, which attracted few birds.

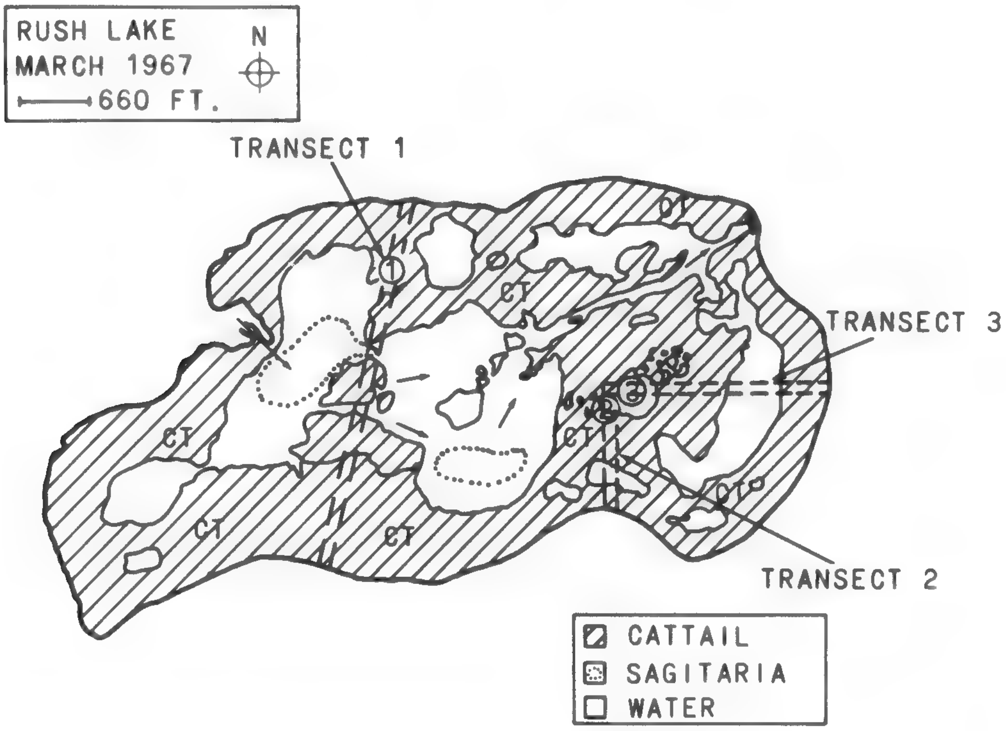


Figure 2. Cover map of Rush Lake showing location of transects, water flow, and cover-water patterns during 1967.

## Appraisal of Muskrat Populations

Because of the impact of muskrats on vegetation for food and lodging, some assessment of their populations was essential. Dozier (1948) found that "lodge" or "house" counts were valuable indices, but Errington (1963) preferred territory counts. Correlations between lodge numbers and open water proved valuable in relating marsh vegetative patterns to bird use in other Iowa marshes (Weller and Spatcher, 1965) and this technique was used at Rush Lake because of similar objectives. We were more interested basically in the impact of muskrats on vegetation and the gross changes in muskrat populations and harvest than in detailed population ecology, which Errington (1963) studied thoroughly.

Lodge counts were made once annually in the winter by a crew traversing the ice

Table 1

Size and Frequency of Openings in Emergent Vegetation, Rush Lake, 1964-1970

| *Diameter of opening in feet* | *Number of openings by year* | | | | | | |
|---|---|---|---|---|---|---|---|
| | *1964* | *1965* | *1966* | *1967* | *1968* | *1969* | *1970* |
| 2–5 | 58 | 861 | 632 | 847 | 598 | 168 | 12 |
| 6–10 | 10 | 112 | 109 | 123 | 97 | 68 | 17 |
| 11–25 | 7 | 47 | 48 | 46 | 40 | 60 | 20 |
| 26–50 | 3 | 7 | 17 | 15 | 15 | 18 | 5 |
| 51–100 | | 2 | 2 | 5 | 8 | 7 | 6 |
| 101–150 | | 1 | 1 | 3 | 3 | 4 | 2 |
| 151–200 | | 1 | 0 | 0 | 1 | 1 | 1 |
| 201–250 | | | 1 | 1 | 0 | 3 | 0 |
| 301–350 | | | | | 0 | 1 | 2 |
| 401–450 | | | | | 2 | 0 | 1 |
| 451–500 | | | | | | 1 | 0 |
| 601–650 | | | | | | 1 | 1 |
| 751–800 | | | | | | 1 | 0 |
| 851–900 | | | | | | | 1 |
| 901–950 | | | | | | | 1 |
| 1,101–1,150 | | | | | | | 1 |
| Total number of openings | 78 | 1,031 | 810 | 1,040 | 764 | 333 | 71 |
| Size range of areas 2 feet or larger | 1–46 | 1–154 | 1–204 | 1–229 | 1–421 | 1–769 | 1–1,116 |
| Mean size of areas 2 feet or larger | 5.2 | 3.5 | 4.5 | 4.2 | 6.2 | 19.3 | 95.2 |
| Standard deviation of areas 2 feet or larger | ±7.9 | ±7.5 | ±10.8 | ±11.7 | ±16.2 | ±33.6 | ±225.4 |

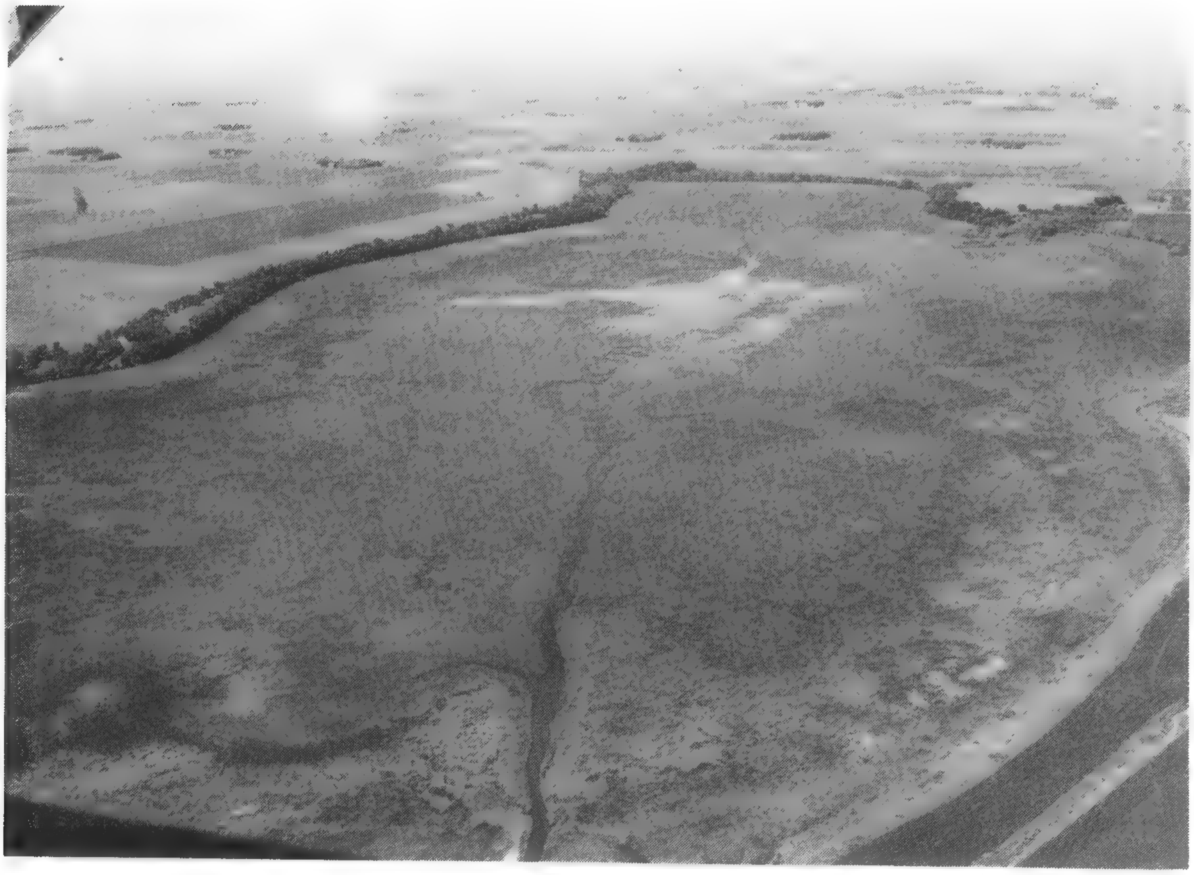


Figure 3. Aerial photograph of Rush Lake in 1965, the first year of reflooding.

and surveying from the wooded knolls, which border the southern edge of the marsh. In addition, winter counts of lodges in transects were made in most years, and often lodges were counted during the summer nest surveys as well.

Harvest data were collected via mandatory reports submitted to the local game manager by trapping permittees.

## *Vegetation*

### Vegetative Patterns and Dynamics

A variety of moist-soil and emergent plants germinated in response to the two summers and one winter of lowered water level, forming a "dense marsh" (terms from Weller and Spatcher, 1965) composed of many annuals or marsh edge perennials, as well as typical deep-marsh perennials. Some openings created by differences in water depth influenced germination and, when reflooded in 1965, pools increased in number and size (Table 1) to form an interspersion of plant cover and water very attractive to marsh birds (Figure 3).

Figure 4 shows the increase in the percentage of points in the marsh at which open water occurred (openings of two feet or larger). This figure demonstrates the drastic, but typical, decline in the amount of emergent vegetation when open water increases. Figure 4 also shows the increase in water areas which exceeded 9, 24, and 49 feet and which may be large enough to influence the selection of nest sites by birds.

Table 1 shows the changes in frequency of occurrence of water areas of various sizes. The maximum number of openings in the emergent vegetation occurred in the period from 1965 through 1968, but these openings were mainly 2 to 10 feet in diameter (Table 1). Cutting of vegetation by muskrats gradually increased the size of some potholes, so that both the number of larger pools and their average size increased, especially during 1969.

Not only did the percentage of open water increase with the duration of inundation, but the distribution of covering vegetation changed as influenced by basin shape, water depth, and muskrat feeding and lodge-building. The central, deeper part of the marsh was open from 1965 on, and the size of this opening increased each year until only a perimeter of vegetation remained in 1970.

## Emergents

Vegetative point-count data for all three transects are summarized in Figures 5, 6, 7, and 8 and Table 2, by life form and species or genera. The cattail *Typha* is clearly the dominant emergent in frequency of occurrence in all but the first year of sampling (1964). After flooding, cattail exceeded the totals of all other plants. This form is the hybrid of *T. latifolia* and *T. angustifolia,* which dominates most marshes of central and northern Iowa (see Smith, 1967 for a review of the taxonomy of *Typha*). Although we found some pure *T. latifolia* in 1965 and 1966, this shallow-water plant disappeared rapidly with the 16- to 30-inch water depths common at Rush Lake. The hybrid form regularly tolerates depths up to 30 inches.

The vegetative propagation of a dense cattail stand from initially sparse germination is demonstrated by using data from point-count transects as an index to density. In analyzing the data, we considered uninterrupted stands of vegetation by excluding open water areas larger than 10, 25, and 50 feet,

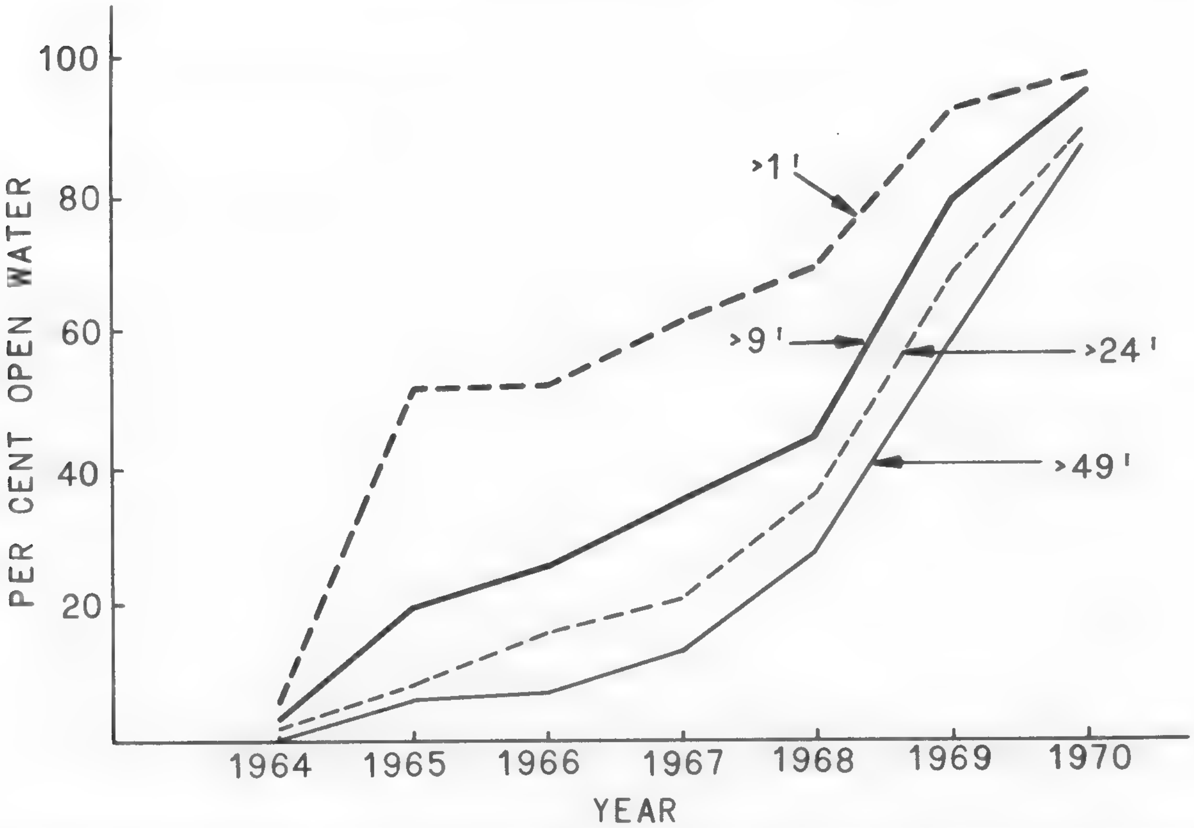


Figure 4. Percentage of open water based on point-count transects summarized by various minimal sizes of openings, 1964–1970. Curves represent different sized openings: greater than one foot, greater than nine feet, greater than 24 feet, and greater than 49 feet.

## Table 2

## Species Composition and Abundance of Vegetation of Rush Lake Based on Point-count Transects, 1964–1970

| | *Totals** | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *1964* | | *1965* | | *1966* | | *1967* | | *1968* | | *1969* | | *1970* | |
| Total transect lengths | 6,918 | (100) | 6,948 | (100) | 6,936 | (100) | 6,883 | (100) | 6,740 | (100) | 6,918 | (100) | 6,929 | (100) |
| Upland edge | 70 | (1) | 82 | (1) | 58 | (1) | 69 | (1) | 60 | (1) | 62 | (1) | 65 | (1) |
| Marsh mud-flat | 2,921 | (42) | 74 | (1) | 194 | (3) | 117 | (2) | 0 | (0) | 0 | (0) | 39 | (1) |
| Flooded area | 3,927 | (57) | 6,792 | (98) | 6,684 | (96) | 6,697 | (97) | 6,680 | (99) | 6,856 | (99) | 6,825 | (98) |
| Total points with emergents | 6,498 | (94) | 3,338 | (48) | 3,301 | (48) | 2,551 | (37) | 1,946 | (29) | 416 | (6) | 69 | (1) |
| *Typha* hybrid | 1,180 | (17) | 1,712 | (25) | 2,502 | (36) | 2,348 | (34) | 1,881 | (28) | 416 | (6) | 69 | (1) |
| *Typha latifolia* | 0 | (0) | 17 | (0) | 19 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Scirpus validus* | 1,588 | (23) | 834 | (12) | 310 | (4) | 17 | (0) | 2 | (0) | 0 | (0) | 0 | (0) |
| *Scirpus fluviatilis* | 120 | (2) | 49 | (1) | 27 | (0) | 27 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Cyperus* spp | 540 | (8) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Sagittaria* sp | 1,085 | (16) | 597 | (9) | 282 | (4) | 84 | (1) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Leersia* sp | 201 | (3) | 4 | (0) | 9 | (0) | 3 | (0) | 12 | (0) | 0 | (0) | 0 | (0) |
| *Polygonum* spp | 528 | (8) | 4 | (0) | 6 | (0) | 2 | (0) | 2 | (1) | 0 | (0) | 0 | (0) |
| *Impatiens* sp | 111 | (2) | 5 | (0) | 24 | (0) | 0 | (0) | 6 | (0) | 0 | (0) | 0 | (0) |
| *Bidens cernua* | 911 | (13) | 3 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| Total points with submergents | 1,502 | (22) | 3,004 | (43) | 3,789 | (55) | 1,757 | (26) | 2,278 | (34) | 2,848 | (41) | 614 | (9) |
| Total submergents recorded | 1,502 | (22) | 4,066 | (59) | 3,789 | (55) | 1,757 | (26) | 2,417 | (36) | 3,158 | (46) | 616 | (9) |
| *Potamogeton pectinatus* | 245 | (35) | 856 | (12) | 1,212 | (18) | 337 | (5) | 546 | (8) | 1,425 | (21) | 273 | (4) |
| *Potamogeton foliosus* | 52 | (1) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Ceratophyllum* sp | 182 | (3) | 447 | (6) | 1,678 | (24) | 449 | (6) | 1,328 | (20) | 1,311 | (19) | 129 | (2) |
| *Elodea* sp | 466 | (7) | 0 | (0) | 3 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Najas* sp | 0 | (0) | 84 | (1) | 29 | (0) | 21 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Chara* sp | 115 | (2) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| *Utricularis* sp | 0 | (0) | 736 | (11) | 867 | (13) | 950 | (14) | 525 | (8) | 422 | (6) | 214 | (3) |
| *Hydrodiction* sp | 411 | (6) | 1,943 | (28) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) |
| Total points with floating plants | 225 | (3) | 2,960 | (43) | 4,631 | (67) | 5,236 | (76) | 3,825 | (57) | 2,968 | (43) | 1,269 | (18) |
| Total floating plants recorded | 225 | (3) | 3,459 | (50) | 5,307 | (76) | 5,690 | (82) | 6,162 | (91) | 6,421 | (93) | 1,988 | (24) |
| *Lemna minor* | 184 | (3) | 2,878 | (41) | 4,631 | (67) | 4,892 | (71) | 3,825 | (57) | 2,831 | (41) | 1,253 | (18) |
| *Spirodela polyrhiza* | 25 | (0) | 474 | (7) | 676 | (10) | 798 | (12) | 2,337 | (35) | 1,684 | (24) | 365 | (5) |
| *Riccia* sp | 0 | (0) | 107 | (1) | 0 | (0) | 0 | (0) | 0 | (0) | 1,906 | (28) | 370 | (5) |
| *Ricciocarpus natans* | 0 | (0) | 19 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 5 | (—1) |
| *Wolfia* sp | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 0 | (0) | 51 | (1) |

*Percentages shown in parentheses. Where total floating and submerged plants recorded exceed total points in plant type, more than one plant was recorded at the point.

Table 3
Summary of Point-count Data*

| | *Length of transect with emergent vegetation* | | | *Stems per feet of all emergents* | | | *Stems per feet of Typha* | | |
|---|---|---|---|---|---|---|---|---|---|
| *Year* | *9 feet* | *24 feet* | *49 feet* | *9 feet* | *24 feet* | *49 feet* | *9 feet* | *24 feet* | *49 feet* |
| 1964 | 6,624 | 6,738 | 6,848 | .98 | .96 | .95 | .18 | .18 | .17 |
| 1965 | 5,488 | 6,254 | 6,456 | .61 | .53 | .52 | .32 | .28 | .27 |
| 1966 | 5,111 | 5,788 | 6,389 | .65 | .57 | .52 | .49 | .44 | .39 |
| 1967 | 4,739 | 5,385 | 5,880 | .54 | .47 | .43 | .50 | .44 | .40 |
| 1968 | 3,646 | 4,220 | 4,781 | .54 | .47 | .41 | .52 | .45 | .39 |
| 1969 | 1,339 | 2,148 | 2,750 | .31 | .19 | .15 | .31 | .19 | .15 |
| 1970 | 214 | 570 | 749 | .32 | .12 | .09 | .32 | .12 | .09 |

*Showing (1) the length of the transect that was vegetated in relation to the size of openings, and (2) the calculated densities of emergent vegetation and cattail (*Typha*) based on various sizes of openings.

and calculating the plant density as mean stems per point (Table 3). Average stem density of all plant species declined gradually from 1964 to 1969. However, cattail showed a gradual increase, reflecting increased stem density until 1969 when there was a sudden decline in density but complete dominance in species present.

*Scirpus validus* was a dominant plant during the period of germination but gradually disappeared due to high water. In general, it germinated on mud flats inside the remaining perimeter of cattail where it was exposed to depths of 12 to 30 inches after reflooding. There is considerable evidence for hybridization in the round-stemmed bulrushes (Smith, 1969) and this may have been a factor in the water tolerance of this population as opposed to its rapid elimination at other glacial lakes (see Weller and Spatcher, 1965). River Bulrush (*Scirpus fluviatilis*) was more widely distributed along the edge of the marsh and survived several years of inundation.

*Sagittaria* was present in all three transects as an open water, rather than marsh-edge, plant growing on silt deposited from the stream. It proved remarkably water tolerant and even flowered in three feet of water.

Moist-soil plants like *Cyperus* sp., *Leersia* sp., *Polygonum* spp., *Impatiens* sp. and *Bidens cernua* mostly disappeared in the first or second year after flooding (1965 or 1966) except along the shore zone (Table 2 and Figure 6). Very little *Carex* existed even in 1964 and almost none can be found along the perimeter because of the abrupt shoreline of the marsh.

### Floating Plants

The frequency of occurrence of floating plants was only three per cent of total points checked in 1964 when only 57 per cent of the transect was flooded (Table 2). Average water depth in 1964 along the transects was 3.3 inches compared with 15 to 28 inches in subsequent years (Table 4). In 1965

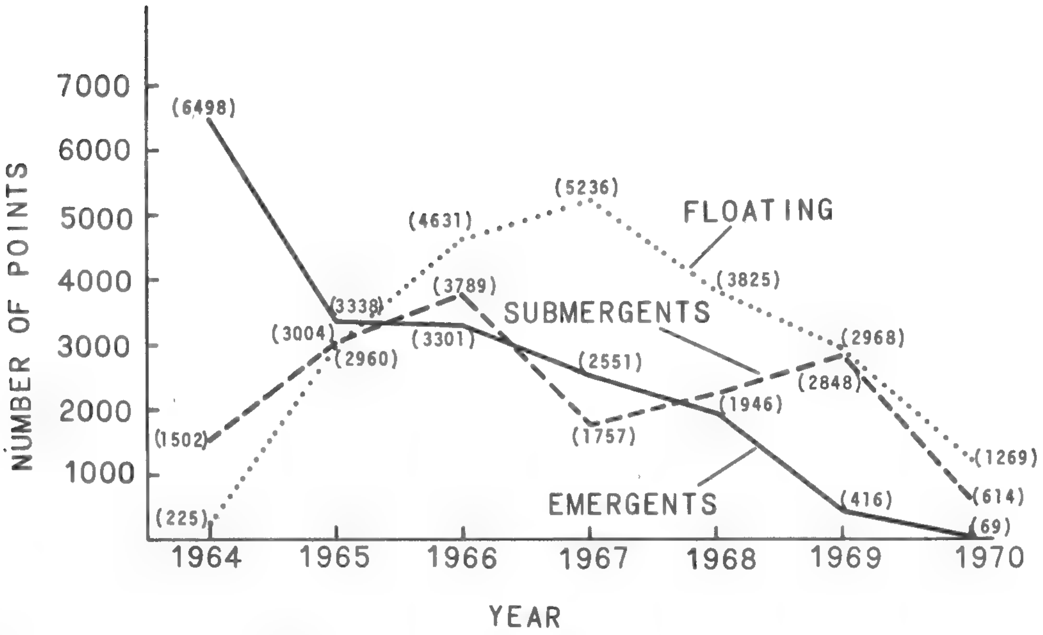


Figure 5. Numerical changes in plant life-forms along point-count transects, 1964–1970.

there was a dramatic increase to 43 per cent of the total points checked for floating plants. High levels of floating plants were indicated even during the later open marsh stages. A reduction in *Lemna minor* in 1968 and 1969 (Figure 7) may have resulted from wind action in open water. *Riccia* showed a general increase late in the flooded stage. Some marshes in late successional or open marsh stage have abundant *Wolffia*, but this was minimal at Rush Lake in 1970.

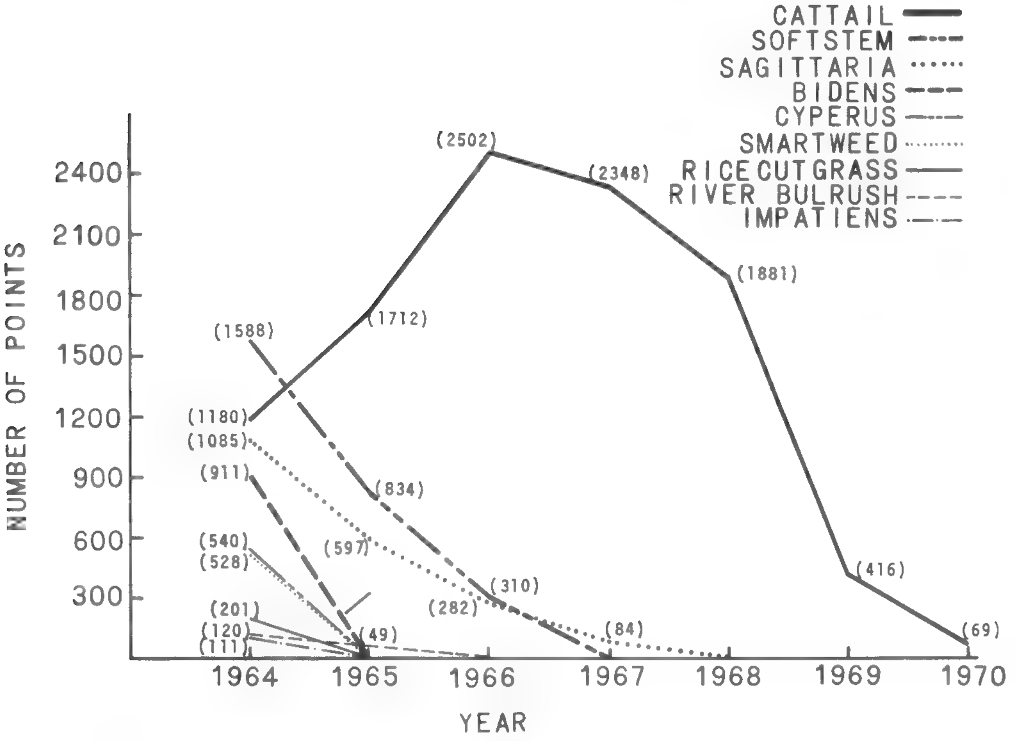


Figure 6. Numerical changes in emergent hydrophytes along point-count transects, 1964–1970.

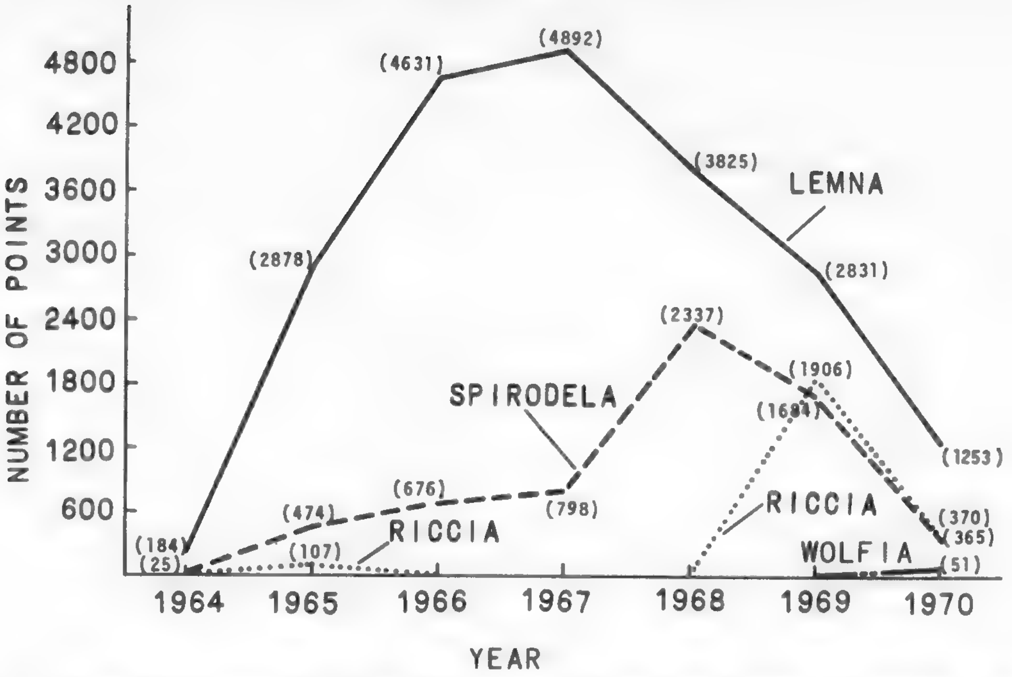


Figure 7. Numerical changes in floating vegetation along point-count transects, 1964–1970.

## Submergents

Point-count data for submergent plants show some variability, possibly because of fluctuations in water levels and turbidity. All transects were surveyed in late July or early August when plants should have reached maturity. There was a rapid elimination of *Elodea* sp., *Chara* sp., and *Potamogeton foliosus,* which survived in the central pool during 1964, and a concurrent increase in *Potamogeton pectinatus, Ceratophyllum demersum* and *Utricularia* sp. (Figure 8). However, rather dramatic fluctuations occurred in these species, particularly the decline of 1967, which may have been a product of a flood in July. High water levels in both 1968 and 1969 also may have been responsible for the lower frequency of *Utricularia* (Figure 8).

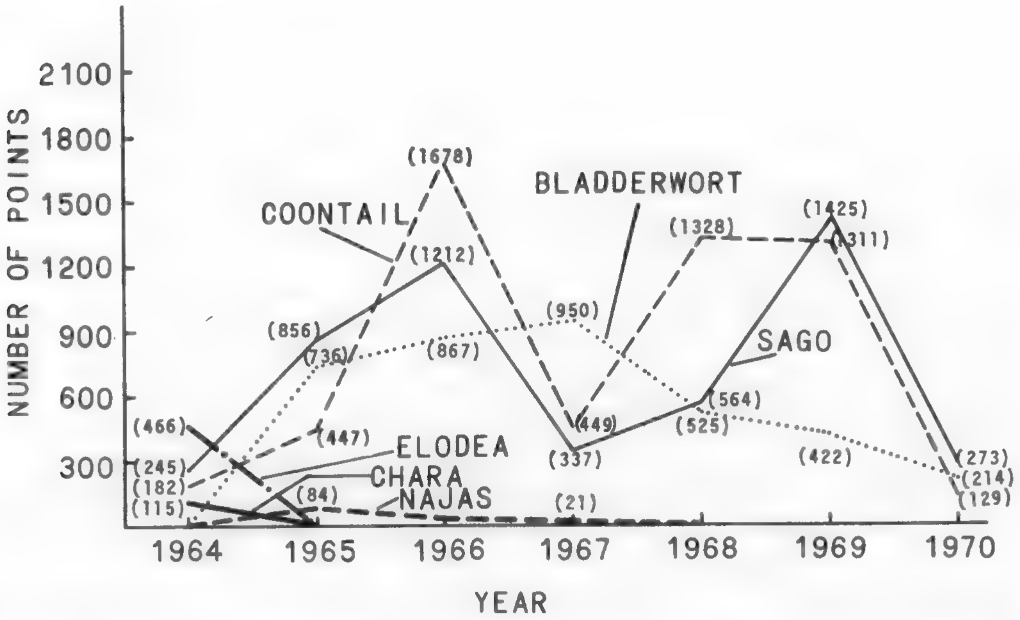


Figure 8. Numerical changes in submergent vegetation along point-count transects, 1964–1970.

Table 4

Water Depths in Inches Along Point-count Transects

| | *1964* | *1965* | *1966* | *1967* | *1968* | *1969* | *1970* |
|---|---|---|---|---|---|---|---|
| Mean | 3.27 | 18.1 | 15.9 | 16.2 | 31.4 | 28.3 | 22.7 |
| Range | 1–12 | 1–27 | 1–28 | 1–21 | 1–40 | 1–36 | 1–32 |
| Standard deviation | ±1.88 | ±4.76 | ±6.76 | ±3.65 | ±6.48 | ±6.13 | ±4.91 |

## *Muskrat Populations*

Data for the muskrat harvest from 1960 to 1963 (Figure 9) showed a decline produced by the draw-down. Thereafter, an explosive increase resulted in excellent trapping success within two years. In 1967, three years after reflooding, lodges dotted the marsh, creating excellent interspersion (Figure 10), and resulting in a harvest of 13.7 muskrats per acre of marsh. The drastic decline in 1968 probably was due to a combination of factors: trapping conditions, lack of proper reporting, habitat changes, and weather conditions.

The decline in lodges in 1968 may be related in part to the maintenance of higher water levels and also to the loss of extensive *Sagittaria* beds in 1967, which muskrats favored for lodge-building in the autumn. Subsequent lodge-building occurred in the perimeter of cattail, which then was in water of sufficient depth to allow the muskrat to use this area through the winter. Heavy snow cover also may have reduced the accuracy of the count.

The general trend in lodge numbers shown in the belt-transects may be more accurate than the figures for the entire lake (Figure 9). Data were not recorded during the first two years but estimates of zero and five, respectively, were made for those years, based on total counts in the entire marsh.

A plot of open water (opening of two feet or greater) recorded in the transects compared with the number of lodges per year (Figure 11) suggests that water openings were present prior to the existence of major openings made by muskrats, presumably a product of patterns of germination and flooding. However, a steady increase in open water during 1966 and 1967 was concurrent with the peak in lodge building.

## *Changes in Bird Populations*

Because some observations had been made on the birds of Rush Lake since 1958, general trends in bird numbers were known, and the impact of the draw-down on populations was especially conspicuous. Data on nests found in transects from 1965 to 1971 are shown in Table 5. No birds nested in 1964 except for a few blackbirds which we did not count. However, data from the 1971 draw-down show a reduction of one-half, even in edge-nesting Red-winged Blackbirds (*Agelaius phoeniceus*), and elimination of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). Blackbirds were not counted in the transects in 1965 and 1967 but, because of a reduced influence of water levels on nesting by Red-winged Blackbirds (see constancy of

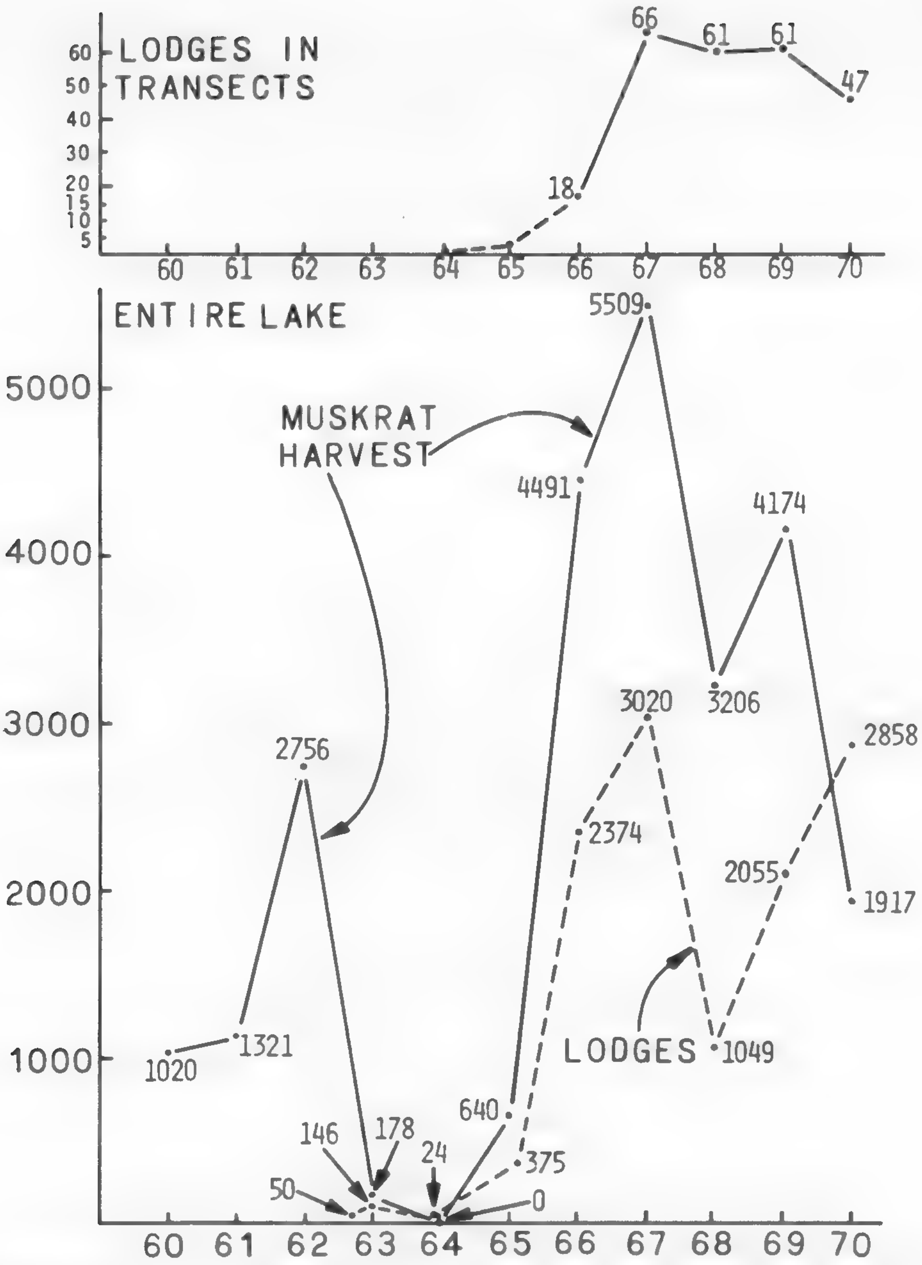


Figure 9. Muskrat harvest and lodge counts on Rush Lake, and lodge counts on 16 acres of belt transects in Rush Lake.

data from other four years in Table 5) and general observations on Yellow-headed Blackbirds, we concluded that numbers of Red-winged Blackbirds were in the 20–25 range in both years and that Yellow-headed Blackbirds ranged from 50–75 in 1965 to 150–175 in 1967

Table 6 provides a somewhat better picture of general numbers and trends in Rush Lake bird populations. This table is based on estimates and extrapolation from transects, but, as previously noted, the figures are especially good for coots, gallinules, terns, and grebes.

Species tended either to respond promptly and significantly to the newly flooded vegetation, or their populations built up slowly over several years as vegetation opened. The lake-wide estimates show a complete absence of birds in 1964, followed by an immediate use of the newly-flooded open pools by coots, grebes, bitterns, and terns. This response was similar to that recorded in the sparse vegetation at Goose Lake near Jewell, Iowa, but a much slower buildup took place at Little Wall Lake because of denser vegetation (Weller and Spatcher, 1965).

Species of the marsh edge, like Red-winged Blackbirds, show greater stability in number, and habitat changes in the marsh had little influence on them because (1) they are inherently more flexible in their requirements, and (2) their nest sites were less severely influenced by muskrats and water levels. However, Yellow-headed Blackbirds, which require water under their nest sites, robust vegetation, and openings in the vegetation, were very sparse in 1964, and increased in the transects from 74 in 1966 to 210 in 1968. Thereafter, the populations declined as muskrats eliminated the habitat, and the 1971 draw-down eliminated all breeding birds from the marsh.

Black Terns (*Chlidonias niger*) found suitable nest sites and foods immediately and declined steadily thereafter as the small-pool complex became open marsh. Forster's Terns (*Sterna forsteri*) responded more slowly, as might be expected because they favor open water areas (Bergman, Swain, and Weller, 1970). Both the transects and estimates for the entire marsh show this general pattern, although there were no Black Terns in the transects in 1965 when they were most abundant in the marsh. Forster's Terns, which are much more social, were disproportionately high in 1968 (seven nests) when they built only 26 nests on the entire marsh. Because such species aggregate in nesting, even a 50 per cent random sample could miss them; hence the value of the general surveys.

Coots seem to pioneer areas rapidly, whereas Common Gallinules tend to move into an area several years after reflooding. In this case, some coots and gallinules were present in all years except when the marsh was dry and dense (1964) and when it was open (1970). Gallinules reached peak numbers in 1967 when coot populations declined. Perhaps the gallinules, which are much less inclined to swim and to nest in semi-open areas than are coots, preferred the lowered water levels. Gallinules also frequent dense vegetation, which was at a very high level in 1967. Possibly, fewer coots reduced interspecific strife and allowed higher gallinule populations.

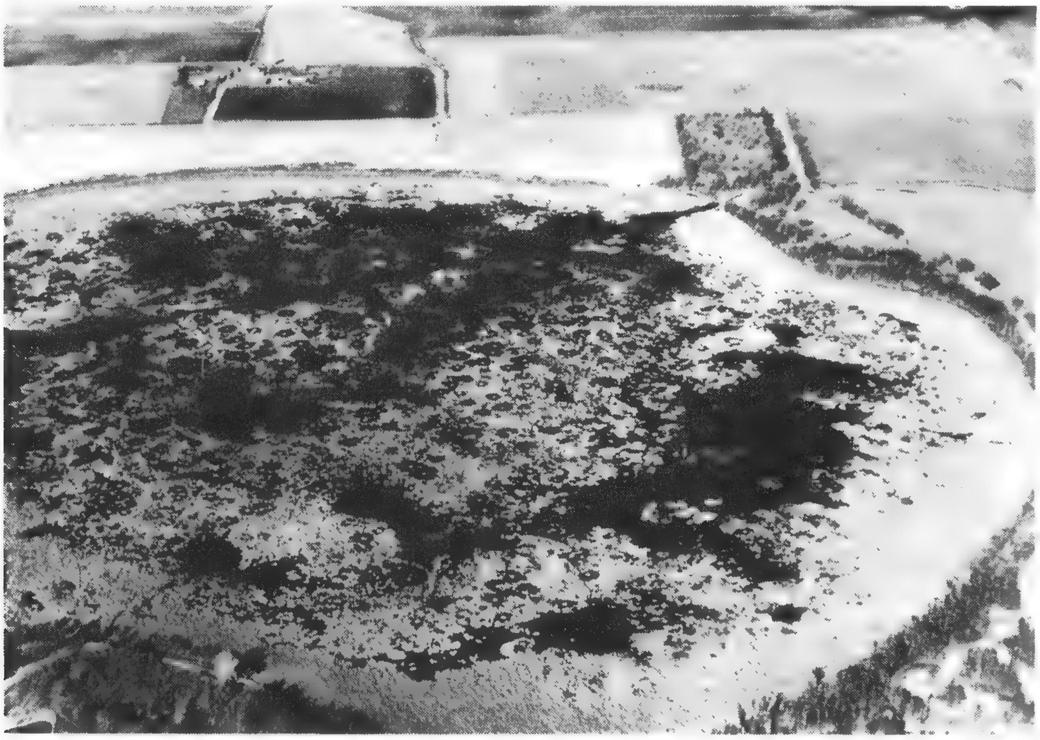


Figure 10. Aerial view of Rush Lake in 1967 showing dispersion of small openings created by muskrat lodge-building.

Table 5

Nests Found in 16 Acres of 3 Belt Transects, Rush Lake, 1965–1970, Supplemented with Data from 1971 Drawn-down Comparable to the Original 1964 Drawn-down

| | *1965* | *1966* | *1967* | *1968* | *1969* | *1970* | *1971* |
|---|---|---|---|---|---|---|---|
| Pied-billed Grebe (*Podilymbus podiceps*) | 6* | 4 | 2 | 1 | 0 | 0 | 0 |
| Black-crowned Night Heron (*Nycticorax nycticorax*) | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Least Bittern (*Ixobrychus exilis*) | 3 | 3* | 1 | 2 | 0 | 0 | 0 |
| Mallard (*Anas playtyrhynchus*) | 0 | 0 | 1 | 1* | 0 | 1 | 0 |
| Redhead (*Aythya americana*) | 2* | 1 | 1 | 2 | 0 | 0 | 0 |
| Ruddy Duck (*Oxyura jamaicensis*) | 0 | 0 | 1* | 0 | 0 | 0 | 0 |
| Ring-necked Pheasant (*Phasianus colchicus*) | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Virginia Rail (*Rallus limicola*) | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Common Gallinule (*Gallinula chloropus*) | 1 | 1 | 2* | 1 | 0 | 0 | 0 |
| American Coot (*Fulica americana*) | 25* | 14 | 3 | 12 | 2 | 0 | 0 |
| Forster's Tern (*Sterna forsteri*) | 0 | 1 | 3 | 7* | 0 | 0 | 0 |
| Black Tern (*Chilodonias niger*) | 0 | 3* | 1 | 0 | 0 | 0 | 0 |
| Long-billed Marsh Wren (*Telmatodytes palustris*) | NR** | NR | NR | 5 | 8* | 0 | 0 |
| Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) | NR | 74 | NR | 210* | 122 | 50 | 0 |
| Red-winged Blackbird (*Agelaius phoeniceus*) | NR | 22 | NR | 25* | 25 | 23 | 11 |

*Suggested peak of species abundance.
**Species present but number not recorded.

Pied-billed Grebes (*Podilymbus podiceps*) responded immediately to the newly flooded areas. A similar response was noted at Goose Lake (Weller and Spatcher, 1965). Thereafter, they declined steadily. This pattern cannot be explained on the basis of our current knowledge, but nesting materials may have been especially abundant during the first year of flooding. A study of their food would have been especially interesting, because fish probably were not at their peak abundance during that first year but frog tadpoles probably were plentiful.

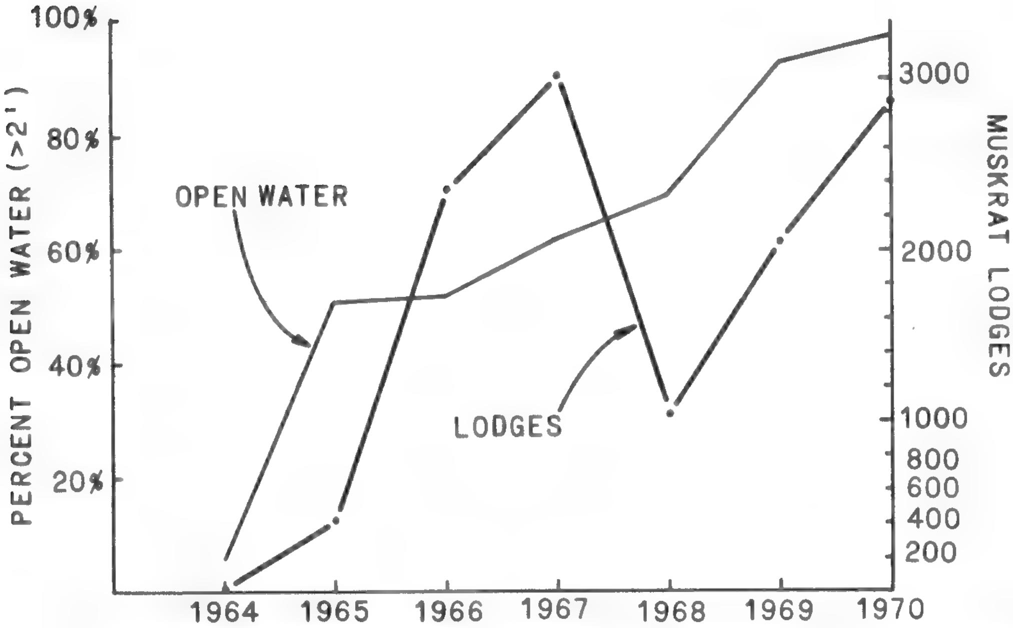


Figure 11. Relationship between muskrat lodges and percentage of open water along transects.

Waterfowl populations were generally the lowest in density of all species but Redheads (*Aythya americana*) and Ruddy Ducks (*Oxyura jamaicensis*) responded to the hemi-marsh conditions from 1965 to 1967. Mallards (*Anas platyrhynchos*), which utilized muskrat lodges for nest-sites, maintained their numbers during the marsh conditions of 1968 to 1970, whereas the diving ducks declined greatly (Table 6).

Least Bitterns (*Ixobrychus exilis*) used the semi-open marsh immediately and were lowest in numbers in 1967 when water levels were low. Data for rails and Long-billed Marsh Wrens (*Telmatodytes palustris*) were not sufficiently accurate to be significant. The nest of the Black-crowned Night Heron (*Nycticorax nycticorax*) was a rarity; few have nested in cattails in Northwest Iowa since the population reported by Bennett and LaMar (1937).

## *Bird-Vegetation Relationships*

Semi-permanent glacial marshes appear to reach their peak of avian production during the hemi-marsh stage when emergent-cover-to-water ratios are about 50:50 (Weller and Spatcher, 1965). However, this is a crude estimate and, as can be seen in figures on pothole size (Table 1 and Figure 4), the method of measuring plant density and patterns of dispersion influence the resulting ratios. In the study of Goose and Little Wall Lakes, where we made cover maps and calculated ratios by use of a planimeter, point-count transects were used as an index to density and to measure the major breaks (pools) in emergent vegetation. Pool size varied dramatically and calculations of vegetation-to-open-water ratios and plant density depended upon the size of the pool considered. Hence, several sizes were used in Figure 4 in searching for the most meaningful correlation. Using any break between three points (i.e. a two-foot opening), the cover-to-water ratio in the first year of flooding (1965) already was 52 per cent water to 48 per cent cover. Using the smallest measurable pool size from the point-count

## Table 6

### Estimates of Breeding Populations of Birds, Rush Lake, 1962-1971*

| *Species* | *1962* | *1963* | *1964* | *1965* | *1966* | *1967* | *1968* | *1969* | *1970* | *1971* |
|---|---|---|---|---|---|---|---|---|---|---|
| Pied-billed Grebe | <10 | <5 | 0 | 132** | 88 | 44 | 24 | <10 | 0 | 0 |
| Least Bittern | <20 | <5 | 0 | 66 | 66** | 22 | 48 | <10 | <5 | 0 |
| Mallard | <10 | < 10 | <5 | 20 | 20 | 22** | 24 | 20 | <20 | 0 |
| Redhead | <10 | 0 | 0 | 44** | 22 | 22 | 15 | <10 | <10 | 0 |
| Ruddy Duck | <5 | <5 | 0 | <10 | <10 | 22** | <5 | <5 | <5 | 0 |
| Virginia Rail | <20 | <10 | <10 | 22** | <10 | <10 | 15 | 20 | 20 | 0 |
| Common Gallinule | <10 | <5 | 0 | 22 | 22 | 44 | 24 | <10 | 0 | 0 |
| American Coot | <10 | <5 | 0 | 550** | 320 | 66 | 285 | 48 | <10 | 0 |
| Forster's Tern | <20 | <5 | 0 | <10 | 22 | 26 | 40** | <10 | 0 | 0 |
| Black Tern | <10 | <5 | 0 | >200** | 66 | 75 | 50 | 20 | <5 | 0 |
| Long-billed Marsh Wren | NR | NR | NR | NR | NR | NR | 120 | 190 | <10 | 0 |
| Yellow-headed Blackbird | <500 | <100 | <100 | <500 | 1,625 | 4,000 | 5,000** | 2,900 | 1,150 | 0 |
| Red-winged Blackbird | 500 | 500 | 300 | 500 | 506 | 525 | 593** | 593 | 529 | 150 |

*Includes data from draw-downs of both 1964 and 1971. Estimates based on nests in transects, and nests, brood counts, and general observations outside transects.

**Suggested peak of species abundance.

data as a measure of the per cent of open water, bird species diversity was greatest when the cover-to-water ratio was between 50 and 70 per cent (Figure 12). Dry vegetation (1964 and 1971) and open marsh conditions (1969 to 1970) fill the habitat requirement of only a few species, so these years are consistently low for all species.

A plot of the number of bird species against the number of pools of any size is not easily interpreted because pool sizes influence available nesting cover and interspersion (Figure 13). Figure 13 suggests that birds made little use of the marsh when there were few pools (1964) or large pools approaching open marsh (1969 to 1970). However, bird species diversity reached a maximum in years when many small pools were abundant and interspersed.

Swimming birds like coots adapted to the newly-flooded, sparsely-vegetated post-draw-down stage readily (Figure 14). As plant densities increased (Table 3) with little increase in openings (Table 1), coot populations declined. However, water levels were low in 1967 and this may have been an influential factor. Interconnected pools between dense cattail were attractive to some swimming birds as shown by the increase in numbers of Redheads and Ruddy Ducks (Table 6) during the same period.

Although population data are not available for every year for all species, a relationship between the nesting population of a species and the percentage of open water can be shown. This is especially clear-cut for Yellow-headed Blackbirds (Figure 15), but less so for Red-winged Blackbirds (Figure 16) because their marsh-edge nest substrate was not eliminated. Even in 1971, the reduced height of cattail, which was downed by late winter snowstorms, may have influenced the drastic decline of Red-winged Blackbirds. Coots were most abundant at a cover-to-water ratio of 50:50; whereas Yellow-headed Blackbirds peaked at 70 per cent open water.

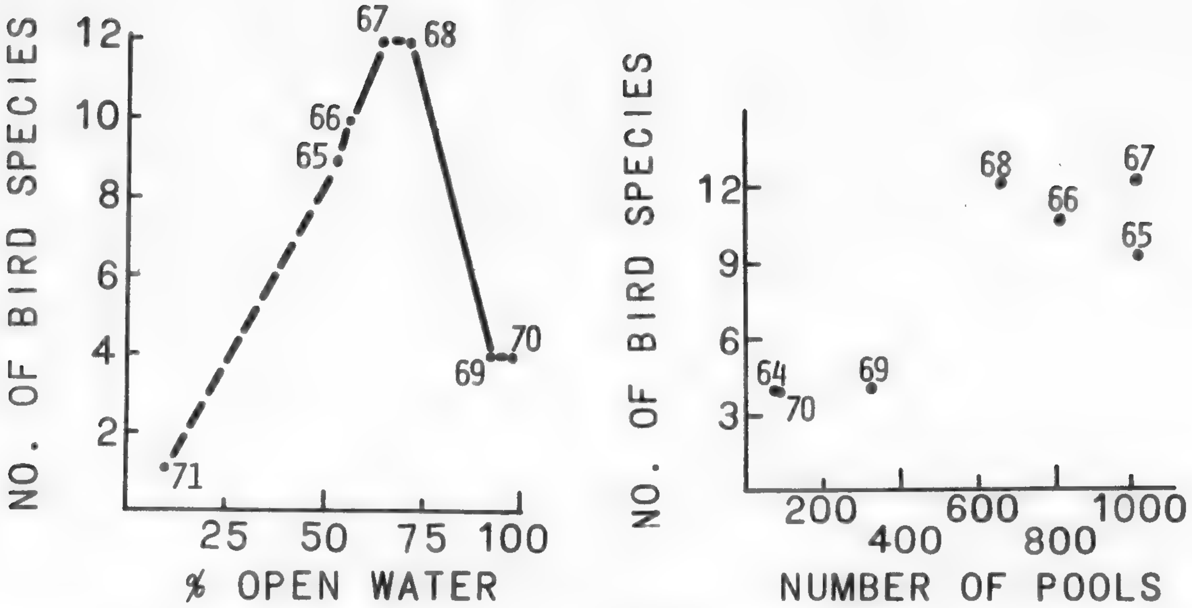
Because the water supply was more regular than in most shallow basins that depend upon rainfall within small watersheds, draw-down and reflooding of Rush Lake were out of phase with regional rainfall cycles, water levels, and habitat cycles at marshes within 20 miles. Comparative data on bird populations from a series of unmanaged pothole marshes in Dewey's Pasture, north of Ruthven, Iowa (about 16 air miles from Rush Lake) serve as a control (Table 7). These potholes were productive in 1964 when Rush Lake was dry. In 1968, Dewey's Pasture was virtually dry and had few or no marsh birds, but Rush Lake was still very productive and at its peak for some species. Therefore, habitat conditions uncharacteristic of the region as a whole made Rush Lake a uniquely attractive entity for marsh birds.

## *Discussion*

### Vegetative Patterns

Observations at Rush Lake show a general pattern of changes in the marsh vegetation and the concomitant effects on bird and muskrat populations from the draw-down-germination phase to open marsh. These data amplify similar data from other lakes in Iowa but better quantify the density and interspersion of emergent plants. Furthermore, the Rush Lake study results from direct experimentation rather than natural change.

Although these reported changes refer to only one lake, general observations of several areas over a period of 12 years confirm that the following



Figures 12 (*left*) and 13 (*right*). At left, the number of bird species in transects is plotted against percentage of open water. The figure at right shows the relationship between the number of bird species and the number of openings in emergent vegetation greater than two feet. Plotted points and numbers represent the years.

pattern of change occurs in plant distribution and density: A marginal stand of robust emergents such as cattail or bulrush often survives both flooding and muskrats. In response to a natural or experimental draw-down, germination produces a sparse stand of diverse semi-aquatic and terrestrial plants in the central unvegetated marsh. Subsequent flooding reduces terrestrial and shallow marsh plants and encourages semi-aquatic perennials such as cattail. The result is a stand of emergents of increasing density but decreasing species diversity. Subsequently, variation in plant density is dependent upon water depth and, presumably, nutrient recycling.

These data also demonstrate that even sparse germination of water-tolerant plants may produce a stand of low density cover attractive to coots and grebes for nesting. Later, plant density becomes so great that movement may be inhibited and pools become of greater importance. Our general impressions are that all marsh organisms respond to these water and habitat changes so that the ecosystem dynamics are visible on a short term scale. Changes in invertebrates undoubtedly are a key factor in determining the use of the marsh by birds.

The following relative conditions describe semi-permanent marshes: (1) Germination phase, prevalent on mud flats or in water less than two inches deep; (2) Newly flooded, with sparse and often well-dispersed vegetation, annuals and immature perennials dominating; (3) Flooded, dense marsh, dominated by perennials; (4) Flooded, hemi-marsh, involving openings in dense emergents; (5) Deep, open marsh, rimmed with emergents.

## Marsh Habitat Diversity and Bird Use

Marshes resemble grasslands in lacking dramatic vertical layering of plant strata, which seem to determine species diversity (MacArthur and MacArthur, 1961). However, at least three strata are used for nest sites: (1a) at

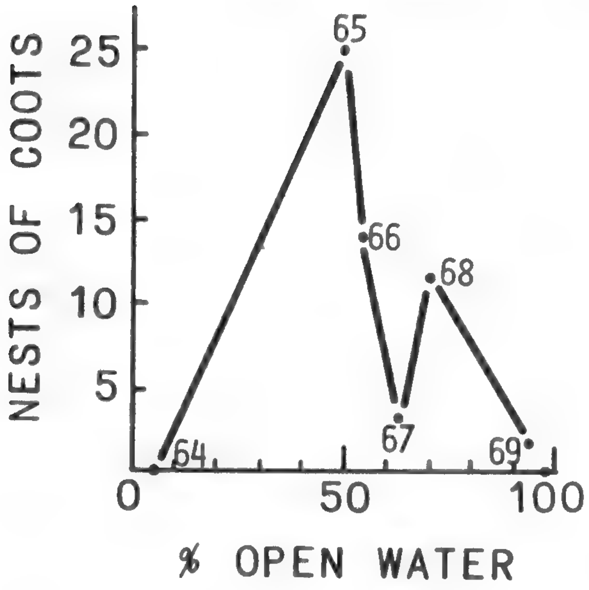


Figure 14. Relationship of the number of coot nests to the percentage of open water in transects. Years shown at points.

water level without emergent vegetation, in which vegetation (often floating debris or submergents) is important only for nest construction — Pied-billed Grebe and Black Tern; (1b) at water level, nest built in emergents such as sedge or cattail — coots, rails, and ducks; (2) above the water level but in short and weak vegetation like sedges — wrens and Red-winged Blackbirds; and (3) above the water level in tall cattail and similar robust emergents — Yellow-headed Blackbird and Least Bittern.

In addition, each marsh has a gradient in water depth, which produces a horizontal zonation that may involve marsh edge trees or shrubs, marginal sedge meadow, central robust emergents, and open water. The deeper parts of the marsh often are not vegetated even during droughts, because they hold water and reduce germination. Muskrats successfully over-winter in the center of marshes where lodges are built in deeper water. Therefore, the pattern of elimination of emergents by muskrats is from the center of the marsh to the periphery. The central pool promotes the use of the marsh

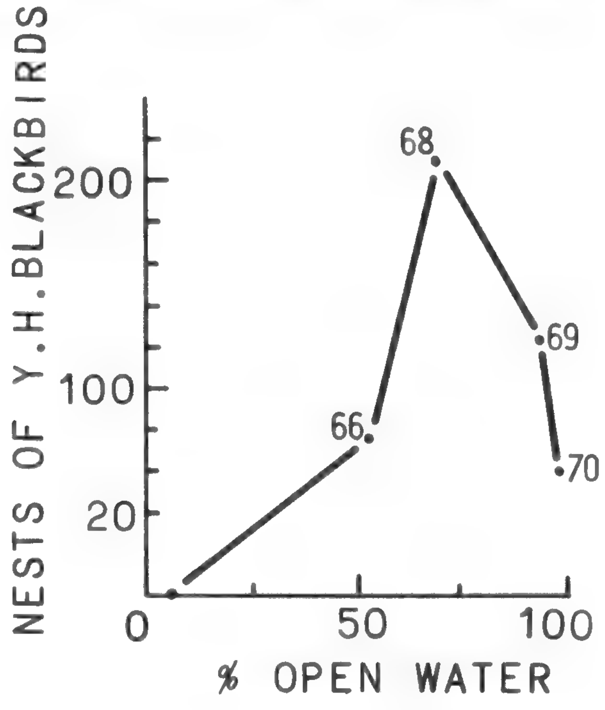


Figure 15. Relationship of the number of Yellow-headed Blackbird nests to the percentage of open water in transects. Years shown at points.

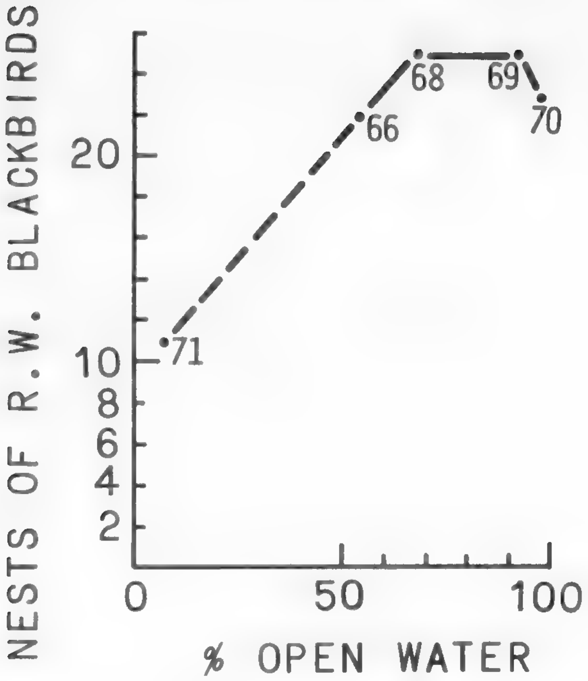


Figure 16. Relationship of the number of Red-winged Blackbird nests to the percentage of open water in transects. Years shown at points.

by birds as soon as the adjacent vegetation is flooded to a depth attractive to certain birds for nesting.

Horizontal zones of vegetation produce a related zonation of birds: (1) Peripheral trees and shrubs host the Red-winged Blackbird and other terrestrial species: (2) peripheral marsh emergents contain the American Bittern (*Botaurus lentiginosus*), rails, marsh wrens, and the Red-winged Blackbird; (3) central robust emergents attract the Pied-billed Grebe, Least Bittern, Redhead, Ruddy Duck, American Coot, Common Gallinule, and Yellow-headed Blackbird; (4) open pools are used by Pied-billed Grebes where nest materials are available and Black Terns and Forester's Terns where suitable substrates exist.

Horizontal zonation is further modified by social behavior where two species compete. Red-winged Blackbirds are forced out of central marsh emergents by aggressive behavior of Yellow-headed Blackbirds (Orians and Willson, 1964; Weller and Spatcher, 1965).

## Succession and Productivity

Although the classical concept of marshes tends to be one of an eutrophic stage of a senescent oligotrophic lake, it is obvious that many marshes have never been deep lakes. Rather, many glacial lake-marsh basins probably have changed little for thousands of years except in relation to surrounding vegetation and general climatic conditions. Although the long-term pattern may be that of a shallow lake progressing through eutrophication to a dense marsh or even a terrestrial system, the short-term pattern is that of an unstable ecosystem with extreme, short-term fluctuation from the near-terrestrial to near-aquatic system. As a product of water availability, this habitat "cycle" is reversible and may last as few as five years or as many as 20. Our general impressions are, however, that few basins inundated over seven years (five is probably a better figure) remain productive of semi-aquatic vertebrates. The usual product of stability is a centrally open marsh with a perimeter of dense cattail or other robust emergent that is generally low in productivity of invertebrate and vertebrate life. We have come to speak of these marshes, ornithologically, as "dead." They lack the lushness and diversity normally associated with temperate, semi-permanent glacial marshes. We believe that insects and other invertebrates and aquatic vertebrates also have dynamic patterns of numerical and spatial changes reflecting complex energy cycles and food webs. Studies of invertebrate populations in relation to the marsh habitat cycle already have started (Voigts, 1973), and truly aquatic vertebrates like fish also need to be considered. One logically concludes that the recycling of nutrients and the germination of new, diverse plants is essential to the rejuvenation of the marsh. In nature, this recycling is produced by droughts and creates problems to wildlife managers, hunters, and fishermen, because the cycle often is one they cannot control. Unfortunately, however, marshes with water control structures often are among the most poorly managed, because public pressure dictates a local preference other than the changing pattern less attractive to the layman. Laymen confuse stability with continued productivity; in most semi-permanent glacial marshes, however, stability of water levels means a lake-type ecosystem which may be productive of fish but not conducive to marsh birds and muskrats.

## Marsh and Marsh-Bird Conservation

Marsh bird populations are no less dynamic than the marsh substrate. Although many factors may influence populations, we are convinced that large marshes attract populations of birds by their habitat features and food supplies, as shown by the 400-acre Rush Lake. Undoubtedly, this is

Table 7

Number of Nests of Marsh Birds in Potholes of Dewey's Pasture, an Unmanaged Control Area, 1964-1970

| *Species* | *1964* | *1965* | *1966* | *1967* | *1968* | *1969* | *1970* |
|---|---|---|---|---|---|---|---|
| Pied-billed Grebe | 15 | 49 | 21 | 17 | 0 | 16 | 18 |
| American Bittern (*Botaurus lentiginosus*) | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| Least Bittern | 1 | 2 | 4 | 6 | 0 | 0 | 2 |
| Redhead | 7 | 10 | 8 | 1 | 0 | 4 | 4 |
| Ring-neck Duck (*Aythya collaris*) | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Ruddy Duck | 2 | 9 | 4 | 2 | 0 | 1 | 2 |
| Virginia Rail | 3 | 9 | 15 | 5 | 0 | 3 | 3 |
| Sora (*Porzana carolina*) | 0 | 7 | 5 | 0 | 0 | 15 | 3 |
| Common Gallinule | 7 | 3 | 1 | 1 | 0 | 0 | 1 |
| American Coot | 36 | 74 | 20 | 9 | 0 | 61 | 26 |
| Totals | 71 | 164 | 79 | 41 | 0 | 101 | 61 |

more true of highly social species with small territories than of wide ranging species, such as some ducks and geese. This concept is of considerable significance in management and conservation of marshes and marsh birds. As a result of marsh successional patterns, a static marsh cannot be considered either a logical or desirable goal when managing for productivity or diversity. Moreover, managing for species diversity and using indicator species like Yellow-headed Blackbirds produces the greatest abundance of all species concurrently. Monocultures are impractical and undesirable.

Further data are necessary to: (1) establish the minimal size of units capable of attracting the diversity of birds common to a particular geographic area, (2) determine whether birds return to areas of optimal habitat in preference to natal areas, and (3) quantify the adaptability of various species using the marsh. These and many other questions relating to basic and applied ecology of marsh birds need intensive study if we expect to preserve isolated marsh ecosystems under increasing human pressures for land and water.

## *Summary*

Dominant emergent and submergent vegetation and bird and muskrat populations of a 400-acre semipermanent glacial marsh were studied from 1964 through 1971 to determine the extent and pattern of short-term vegetation change and its impact on bird populations. Water levels were lowered to initiate revegetation of an open marsh and levels then were regulated to maintain maximal use by birds and muskrats. A subsequent draw-down in 1971 produced conditions comparable to those of 1964. The fact that the water vegetative cycles were out of phase with local unmanaged marshes experimentally demonstrated the avian responses to available habitat. Permanent point-count transects showed an initial sparse germination of diverse moist-soil annuals as well as aquatic perennials. All but cattail were eliminated within three years, whereas cattail density increased steadily. Concurrently, pool size and area of open water increased due to an increased muskrat population which utilized cattail for lodges and food. Bird populations changed dramatically in numbers and species, with the greatest number and species diversity present when 50 to 70 per cent of the open water was well-interspersed with emergent vegetation. The general pattern of short-term vegetation-bird succession in this type of marsh is (1) sparse germination of diverse plant species, which may attract many birds when flooded, (2) an increase in density of perennial emergents to form a dense marsh less attractive to birds, (3) an increase in open water resulting from use of the vegetation by muskrats with a resulting increase in numbers and species of birds in the well-interspersed hemi-marsh, until (4) emergent vegetation is eliminated in the central marsh by muskrats and water levels, and bird populations are reduced to those species using the marsh edge. Such successional changes are not permanent but reflect the dynamic changes of an unstable ecosystem.

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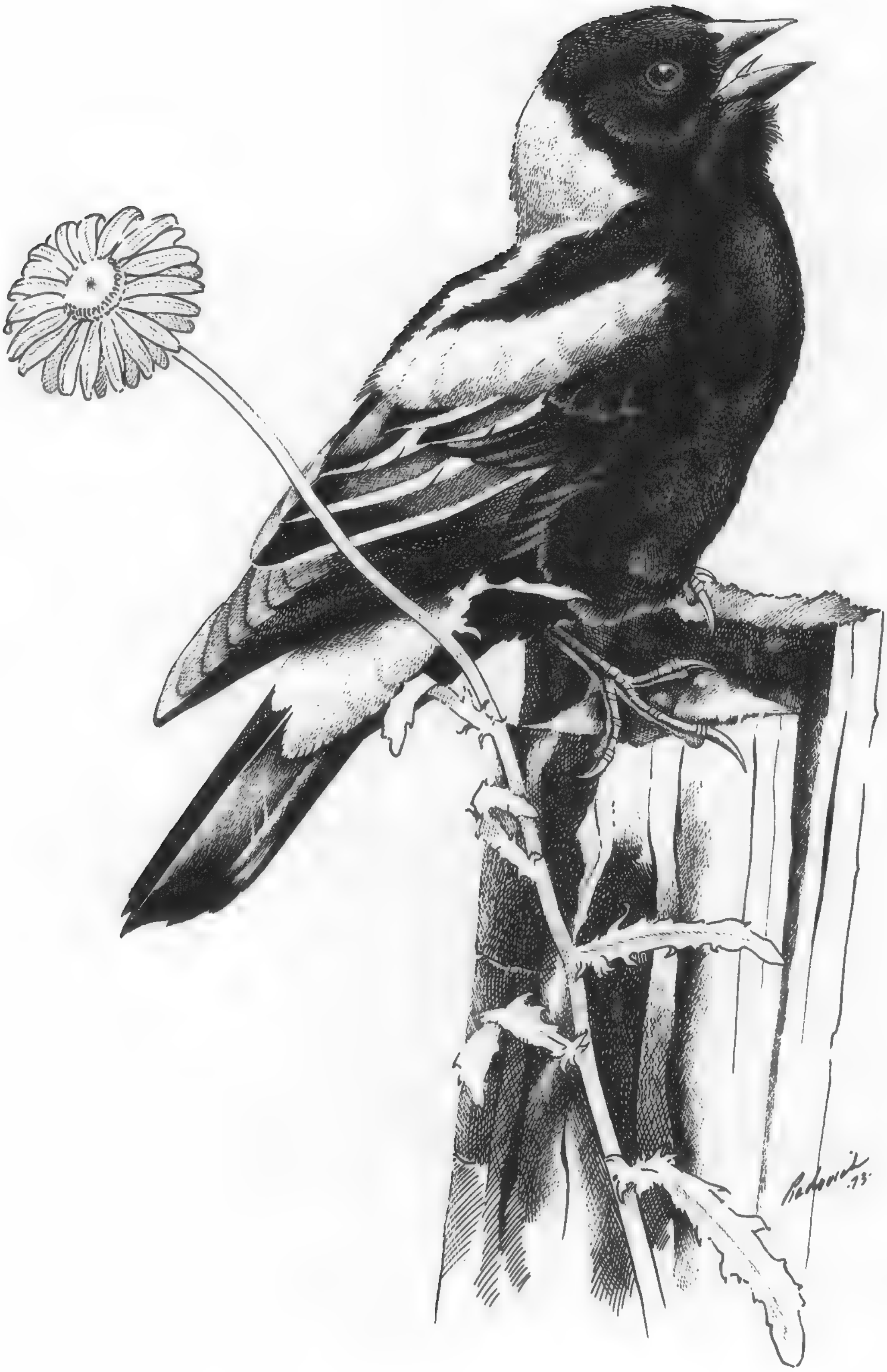
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Bobolink, *Dolichonyx oryzivorus*. Drawing by Don Radovich.

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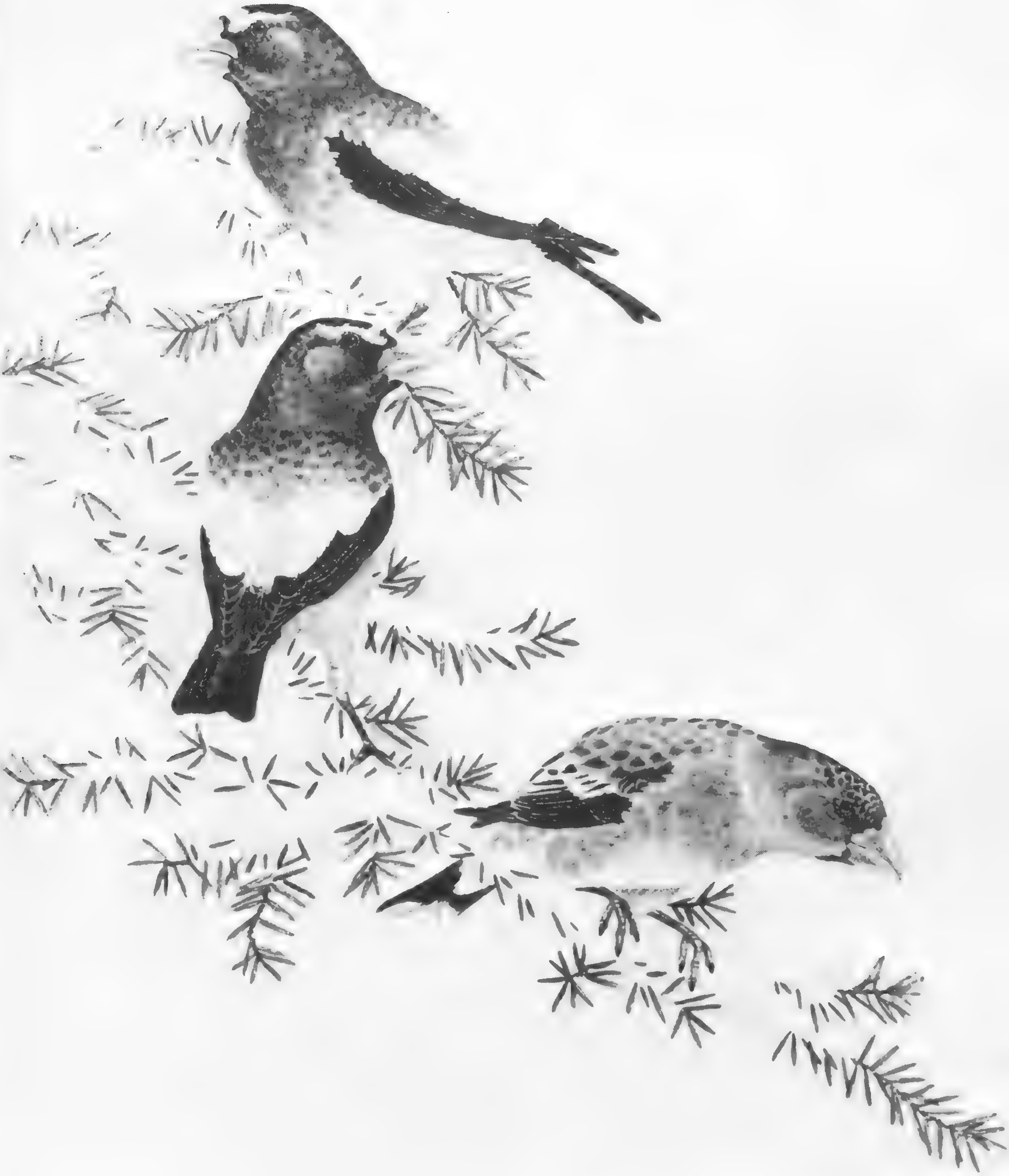

Evening Grosbeaks, *Hesperiphona vespertina.* Painting by John Wiessinger.